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PROBABLE EVOLUTION AND MORPHOLOGICAL VARIATION IN SOUTH AMERICAN DISONYCHINE FLEA BEETLES (COLEOPTERA: CHRYSOMELIDAE) AND THEIR AMARANTHACEOUS HOSTS

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**Probable Evolution and Morphological Variation
in South American Disonychine Flea Beetles
(Coleoptera : Chrysomelidae)
and Their Amaranthaceous Hosts**

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Floating-mat growth habit of alligatorweed. A, Alligatorweed growing in pure stand as floating mats prior to establishment of biocontrol agents at Blue Lake, an oxbow lake, in the Yazoo Basin of the Mississippi River alluvial plain near Itta Bena, Miss. B, The reach of alligatorweed from the floating-mat edge is comparable to the free-floating *Alternanthera hassleriana*, the closest relative of alligatorweed. From the mat margin, erect stems increase in length toward the maximum attained in the mat interior. Compare the length of ascending stems with that shown in figure 7.

Probable Evolution and Morphological Variation in South American Disonychine Flea Beetles (Coleoptera : Chrysomelidae) and Their Amaranthaceous Hosts

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ABSTRACT

PROBABLE EVOLUTION AND MORPHOLOGICAL VARIATION IN SOUTH AMERICAN DISONYCHINE FLEA BEETLES (COLEOPTERA : CHRYSOMELIDAE) AND THEIR AMARANTHACEOUS HOSTS. G. B. Vogt, J. U. McGuire, Jr., and A. D. Cushman. U.S. Dep. Agric. Tech. Bull. No. 1593, 148 pp. *Address communications to G. B. Vogt, Southern Weed Science Laboratory, Science and Education Administration, Stoneville, Miss. 38776.*

Agasicles has an obligatory feeding relationship with three amphibious amaranths, including *Alternanthera philoxeroides* (Mart.) Griseb. There is no danger of host transfer in North America by *Agasicles hygrophila* Selman and Vogt. *Disonycha argentinensis* Jacoby is the closest extrageneric relative of *Agasicles*. These flea beetles diverged from a terrestrial ancestral form resembling *D. argentinensis* and coevolved with the amphibious amaranths. The plants were advanced in their evolution when *Agasicles* appeared. A trifurcate distribution of forms resulted that centers on *A. hygrophila*. The middle arm consists of a polytypic fasciate species, *Agasicles opaca* Bechyné, which overlaps a vittate species, *A. hygrophila*. The four vittate semispecies that comprise the side arms are geographically exclusive and constitute a superspecies. The vittate *Agasicles* species have evolved primarily on alligatorweed centered in the lower basin of the Río de la Plata. Having undergone most of its evolution interacting with small-stemmed alligatorweed, fasciate polytypic *A. opaca* diverged from the vittate forms, continuing its evolution interacting mostly with the oversized stems of *Alternanthera hassleriana* Chod., the closest relative of alligatorweed. While this release from interaction with small stems relates to an accelerated rate of divergence from the vittate forms, it also relates to slowed evolution of reproductive isolation and therefore speciation among the fasciate forms. Normal bivariate ellipses for 11 pairs of characters discriminate taxonomically between some of the vittate semispecies but not between forms of fasciate *A. opaca*. Apparently, interaction with the host-plant stem and the resulting rate of speciation drive the taxon cycle within *Agasicles*. Instrumental in speciation of the genus and concomitant in its evolution has been the seemingly de novo appearance and differentiation of the sexually dimorphic external genitalia. Speciation has not occurred in the other recognized specialized insect biotic agents of amphibious amaranths, which, like *Agasicles*, have geographic ranges that are nearly coextensive with that of alligatorweed in South America. These include *Vogtia malloi* Pastrana and *Amynothrips andersoni* O'Neill, both of monotypic genera, and the leaf-mining *Agromyza alternantherae* Spencer and *Disonycha argentinensis*, both of large polytypic genera. *Disonycha glabrata* (F.) may be the closest intrageneric relative of *D. argentinensis*. Character displacement, also known as ecological shift, may have been the mechanism that led to the divergent host-plant spectra of these two flea beetles. *Disonycha argentinensis* is a more specialized suppressant of terrestrial alligatorweed and should be a more universally effective biocontrol

agent than native North American *D. xanthomelas* (Dalman) and *D. collata* (F.), each of which has a broad host-plant spectrum and is an ecological nonanalog of *D. argentinensis*. The mechanism of character displacement (ecological shift) provides a basis for possible utilization of exotic ecological homologs for weed control. As an alternative to competitive displacement, character displacement could result in coexistence through division of the niche and lead to more effective suppression by both insects because of increased specialization. However, such a process may drive the taxon cycle, and advancement along the cycle could lead to less competitive advantage of the biotic agent in time.

KEYWORDS: *Agasicles*, spp., alligatorweed, *Alternanthera* spp., biogeography, biological control, character displacement, coevolution, *Disonycha* spp., ecological shift, environment, extrinsic coevolution, evolution, flea beetles, host specificity, intrinsic coevolution, morphological variation, normal bivariate ellipses, phenoclines, polytypic species, semispecies, superspecies, taxon cycle.

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The U.S. National Herbarium, one of the five largest herbaria in the world, is an especially rich store of information, most of it unpublished; the field study drew heavily upon it for guidance. Similarly, the Chrysomelidae collections of the Department of Entomology, Smithsonian Institution, were a rich source of study material and geographic records of flea beetles. The remarkable, if not unique, representation of larval Chrysomelidae in those collections was of obvious use in this study. Also, we had access to the important South American collections in the Carnegie Museum, Pittsburgh, Pa., and the American Museum of Natural History.

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INTRODUCTION

Alligatorweed, *Alternanthera philoxeroides*, of the Amaranthaceae, is indigenous to South America but has been introduced into the Southern United States, Puerto Rico,¹ India, Southeast Asia (Sculthorpe 1967),² and Australia.³ In all of these places it has become an economically important aquatic pest. In preparation for biological control of this weed, Vogt carried out extensive field studies on alligatorweed and various related amaranths and their insect predators in South America during 1960, 1961, and 1962. He made additional field studies in South America in 1970 and again in 1975, when Hugo A. Cordo joined him in southern Brazil, Argentina, and Paraguay. Vogt made limited field studies of related amaranths on various trips into the Southern United States, Mexico, and Panama between 1965 and 1971. With P. C. Quimby, Jr., and S. H. Kay, he made extensive field studies in the Southern United States from 1972 through 1977.⁴ During these trips, more than 90 species of insects were found affecting alligatorweed. Of the four South American insects recommended as control agents, three have been introduced into the Southern United States and are successfully combating alligatorweed (Maddox et al. 1971; Brown and Spencer 1973; Blackburn and Durden 1972; Vogt et al. 1975; Spencer and Coulson 1976; Coulson 1977). *Agasicles hygrophila* is one of these insects. This flea beetle and related disonychine species

and alligatorweed and related amaranths are the subjects of this bulletin.

It became evident that *A. hygrophila* and the other vittate species of *Agasicles* have evolved external lock-and-key genitalia that serve to differentiate the species, as shown in figures 2–5 (Selman and Vogt 1971). These features, together with less conspicuous differences in the uncleared aedeagi (figs. 27–30), indicate that these populations are reproductively isolated and are correctly recognized as species. However, the wide-ranging and irregularly variable *Agasicles opaca* (figs. 6 and 9) shows little or no appreciable differentiation of either the external lock-and-key genitalia or the uncleared aedeagi. Additionally, facts about distribution, biology, and morphology obtained during the study pointed to evolutionary relationships between *Agasicles* and certain species of *Disonycha* and to relationships among some of the plant species and also to an intrinsic coevolutionary relation between the insects and their hosts. Evidence of such relationships is discussed in the first part of this bulletin, leading up to proposed evolutionary dendrograms for the flea beetles and plants, and a coevolutionary course is suggested in the second part.

Because of the apparent relationship between flea beetle form and host-plant-stem diameter, Vogt's study included measurements of the internode lengths and stem diameters of 145 specimens of alligatorweed and two closely related amphibious amaranths. All are indigenous South American species, principally of the alluvial lands east of the Andes. These plants are the only known hosts of the five species of *Agasicles*, and with three terrestrial species of *Alternanthera*, they are the only known hosts of the closest extrageneric relative of *Agasicles*, *Disonycha argentinensis* (fig. 1) (Vogt and Cordo 1976). These six flea beetle species, 314 specimens in all, were measured for 22 different dimensions of body and appendages. The data on morphological variation of host plants and insects are summarized and analyzed in the third part of

¹C. F. Zeiger, personal communication, 23 Oct. 1975.

²"Literature Cited" begins on p. 133.

³K. E. Harley, personal communication, 9 Sept. 1976.

⁴Findings of these widespread field studies are reported in detail in manuscripts in various stages of preparation. They are: (1) G. B. Vogt, P. C. Quimby, Jr., and S. H. Kay, "Alligatorweed, Related Amaranths, and Their Biotic Suppressants in the Americas"; (2) G. B. Vogt, P. C. Quimby, Jr., and S. H. Kay, "Field Studies of Flea Beetles, Host Plants, and Lebiine Predator Parasites in the Southern United States"; (3) G. B. Vogt, P. C. Quimby, Jr., and S. H. Kay, "Progress of Biological Control of Alligatorweed in the Lower Mississippi Valley Region"; and (4) G. B. Vogt and H. A. Cordo, "Field Studies of Flea Beetles, Host Plants, and Lebiine Predator Parasites in South America."

this bulletin. Their evolutionary and biogeographical meaning, taxonomic utility, and significance in biocontrol of weeds are discussed in the fourth part.

The purpose of this bulletin is eightfold: first, to present a digest of information on relationships among the flea beetles and their host plants (most of this information was derived from natural history collections and from the field studies outlined above); second, for the three species of amphibious amaranths, to present the variations in stem size in terms of normal bivariate ellipses and relate these to normal bivariate ellipses expressing the variations of external character dimensions of the flea beetles (*Disonycha argentinensis*, each of the four vittate *Agasicles* species, and the fasciate *Agasicles* forms combined under *A. opaca*); third, to apply these ellipses in discriminating taxonomically the five recognized species of *Agasicles*; fourth, to indi-

cate the relationship between the mean values for each set of proportions (x to y) in the evolutionary course of the flea beetle species, supposing that they diverged successively from a common terrestrial ancestral form near *Disonycha argentinensis*; fifth, to present separately the mean points and normal ellipses for three geographic forms of the fasciate *Agasicles opaca* and consider their taxonomic and evolutionary significance; sixth, to recast all of these evolutionary relationships in view of currently developing concepts of the biogeography of South America; seventh, to examine critically the possible coevolutionary course in the host plants that may have diverged simultaneously from exclusively terrestrial plants to become the present-day amphibious plants; and eighth, from the results, to make interpretations that are of importance in the biocontrol of weeds.

RELATIONSHIPS AMONG FLEA BEETLES AND THEIR HOST PLANTS

Some Host-Plant Characteristics

Except possibly *Alternanthera maritima* in southern Florida, there is no species of this genus indigenous to the United States. However, closely related *Philoxerus vermicularis* is probably indigenous along the beaches of the Gulf Coast States (Small 1933; Correll and Johnston 1970). The amphibious amaranths constitute less than 5 percent of the estimated 120 species of *Alternanthera* known from South America and the estimated 170 species known from North America (the West Indies, Mexico, and Central America) and South America combined (Lawrence 1951). Most species are mesophytic or xerophytic; a few are halophytic. In South America, there are three additional species of amphibious amaranths besides alligatorweed, *Alternanthera hassleriana*, *Alternanthera sessilis*, and *Alternanthera reineckii*. *A. reineckii* grows along river courses, in seepage areas, and in wet depressions (rain pools) over much of southern South America. It is limited to regions of campo (Roberto M. Klein in Smith and Downs 1972). We have observed extensive colonies in depressions behind a natural levee along the Tebicuary River in Paraguay and a small colony in a wet meadow in the Province of Corrientes.⁵ These plants were being used only by flea beetles of the genus *Systema*. A fifth amphibious amaranth, *Alternanthera tetramera*, occurs in Brazil,⁶ but we have failed to find this plant; apparently it too occurs in the campos.

According to Engler (1934), alligatorweed and *A. hassleriana* are classified under section I of the subgenus *Telanthera*, while *A. sessilis*, *A. reineckii*, and *A. tetramera* are classified under section I (*Allaganthera*) of the subgenus *Eualternanthera*. From this classification it is apparent that a signifi-

cant divergence has been recognized between these two groups, but not all botanists recognize *A. hassleriana* as distinct from alligatorweed because no demonstrable differences in flower structures between the two plants have been found.

Each of these species grows in a range of habitats from mesophytic terrestrial to aquatic. Most plants are amphibious to the extent of being able to withstand at least partial drying of the habitat for extended periods. Many plants root on banks and shallow bottoms, or often, especially in the case of *Alternanthera hassleriana*, attach themselves to a lagoon bottom by a slender cordlike stem. High water may completely submerge many plants, which often refloat if rooted to peaty bottoms of intermittent lagoons.

East of the Andes, alligatorweed grows over much of South America in a variety of lagoons and ponds and in sluggish to swift-flowing watercourses. Habitats include ditchbanks, point bars along meandering streams and rivers, and margins along trough and oxbow lagoons, backwaters, and distributaries in alluvial plains. In deltas, especially that of the Paraná River, alligatorweed grows ubiquitously in diverse aquatic to subaquatic habitats (Burkart 1957). On higher ground along or near the Paraná River, often on cultivated land, alligatorweed frequently grows as a terrestrial plant with rootlike rhizomes, some appearing like large taproots. Many of these sites are seldom, if ever, flooded. In Pedersen's view (cited in footnote 6), those above flood level may depend upon human activities for establishment, but because alligatorweed does produce viable seed occasionally in southern South America (Vogt 1973), its establishment by natural means cannot be ruled out. *Alternanthera hassleriana* very rarely produces seed and is not known to grow on sites that are free of flooding. Both *Alternanthera sessilis* and *A. reineckii* normally produce abundant seed, and both occur as terrestrial plants above the reach of fluvial floods.

⁵T. M. Pedersen showed us our first colony of *Alternanthera reineckii* in a wet meadow on Estancia Santa Maria, Province of Corrientes, 16 Mar. 1975.

⁶T. M. Pedersen, personal communication, 16 Mar. 1975.

A. sessilis has an ecological range similar to that of alligatorweed. From what we have seen of this plant in the Americas, it may not be an indigenous species. However, in the sub-Andean portion of its range, it is the only amphibious amaranth. The smaller watercourses of this region are deeply shaded by tropical rain forest. Under primeval conditions, the plant may form colonies only where a tree fall creates an opening. The range of this tropicopolitan species extends into the West Indies, Central America, and southern Mexico. It is important to note that *A. sessilis* appears to be more closely related to Southeast Asian species (T. M. Pederson, cited in footnote 6).

The internodes of amphibious amaranths are usually hollow and can thereby provide the flotation needed in some aquatic habitats to keep most of the foliage above water. The tropicopolitan *Alternanthera sessilis* develops the most slender stems of the three species that are known hosts of disonychine flea beetles in South America. *A. hassleriana* is the most highly specialized, having decumbent floating stems with conspicuously inflated, densely pilose internodes (fig. 7). This species is adapted and restricted to insulated river lagoons that fluctuate in level and even dry up for extended periods. The internode pilosity, both when dry and when wetted by a film of water, may protect against the aquatic flea beetle *Agasicles opaca*.

A. obovata is confined to Mexico, Guatemala, and Honduras. Although its flower structure is considered to be very different from that of *A. philoxeroides*,⁷ it has the appearance of being a North American counterpart of the South American indigene. This is probably a coincidence of convergent evolution. Although they have similar growth habits, *A. obovata* has a narrower ecological range than does alligatorweed.

Along the seacoasts of eastern South America, of the Carribean, and of the Gulf of Mexico are two species of *Philoxerus*. These curious halophytic plants are similar in growth habit to alligatorweed. Just as alligatorweed is a pioneer plant of newly deposited silts along freshwater courses, *Philoxerus* is a pioneer along seabeaches.

⁷L. B. Smith, personal communication, 1 Nov. 1967.

Pupation of *Agasicles* Species in Host-Plant Stems

There are no host plants other than amphibious amaranths for the genus *Agasicles* (Maddox et al. 1971; Vogt et al.⁸). A flavone feeding stimulant, isolated from alligatorweed, is involved in the host specificity of *Agasicles hygrophila* (Zielske et al. 1972). All known species of *Agasicles* are limited to the near-saturation humidities of the subaquatic to aquatic habitats of the amphibious amaranths.

Species of *Disonycha* that attack amphibious amaranths are restricted to plants growing on terrestrial sites. These flea beetles are oligophagous to near polyphagous. *Disonycha argentinensis* (fig. 1), *D. eximia*, *D. collata*, *D. xanthomelas*, *D. glabrata*, and several species of the very closely related genus *Phenrica* (fig. 8) are known to attack amphibious amaranths. All of these insects pupate in soil and organic detritus, as do almost all of their known terrestrial allies in the Alticinae.

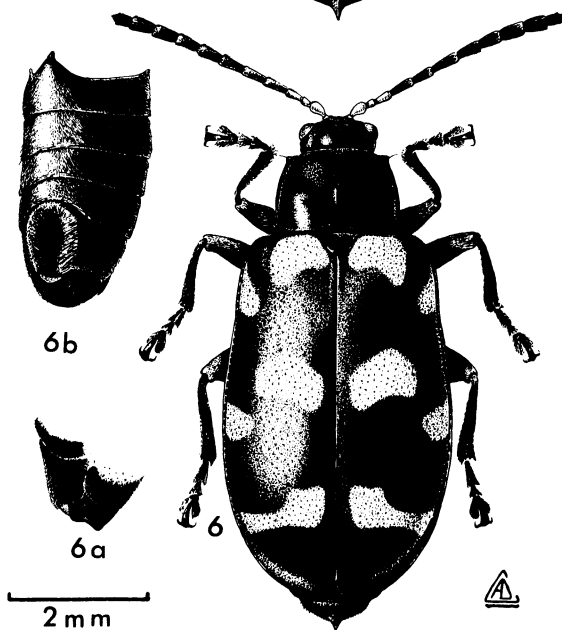
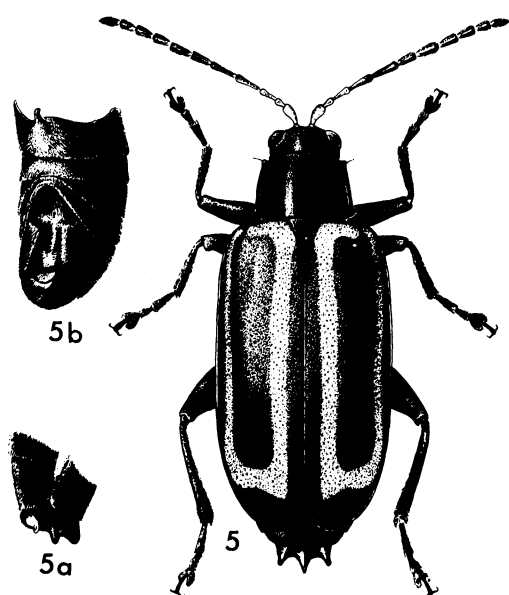
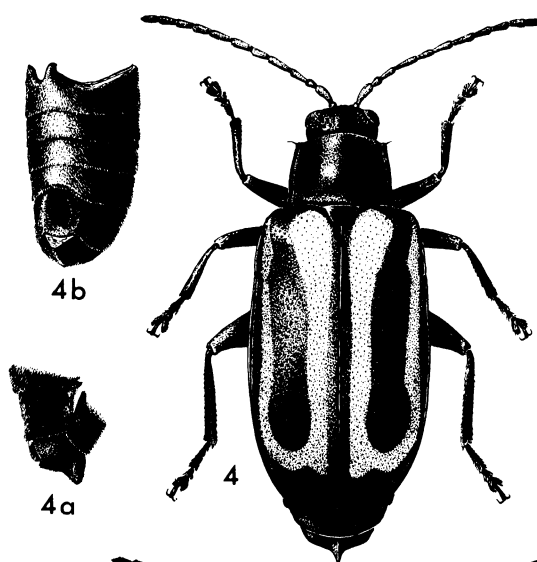
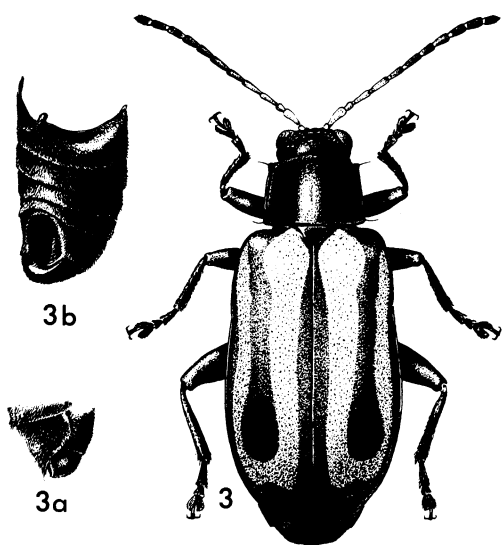
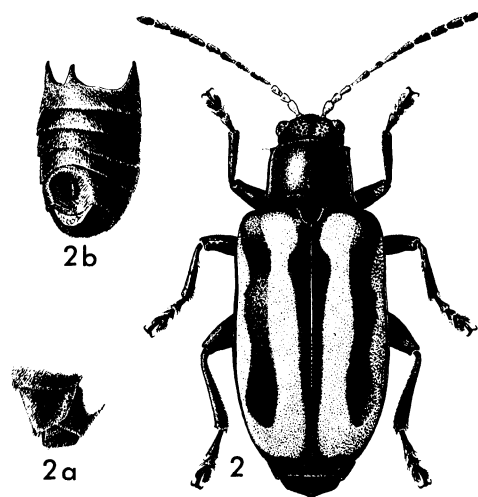
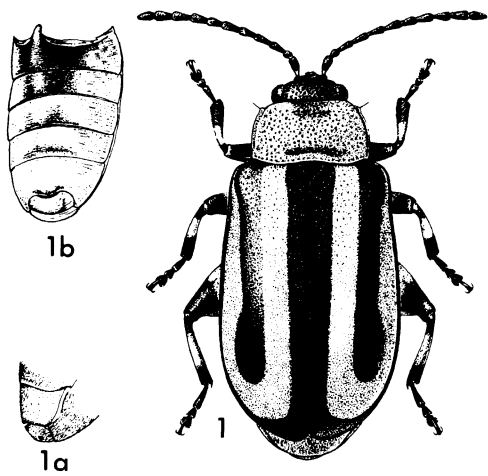
Soil is not usually readily accessible to aquatic flea beetles, and pupation can take place either on an exposed surface, in a manner suggestive of the Coccinellidae, or in the moist to wet soil near the water's edge. *Lysathia flavipes* of South America and *Lysathia ludoviciana* of North America have this facultative behavior. *Agasicles* pupation, on the other hand, occurs only inside the host-plant stem, with the prepupal, slightly larger than head-sized entrance hole being sealed with frass (not fecula) and a binder that may include an anal exudate. However, Maddox (1968) reports that "the ingested [probably not beyond the foregut] stem tissue from the entrance hole is masticated and regurgitated to form a plug, and the plug is molded along the perimeter of the hole by using the pro[thoracic] legs and head. Some tissue used to form the plug is also derived from the inside walls . . ."

The developing flea beetle inside the stem is well protected from rising waters that result in sub-

(Continued on page 10.)

⁸G. B. Vogt, P. C. Quimby, Jr., and S. H. Kay, "Alligatorweed, Related Amaranths, and Their Biotic Suppressants in the Americas" (in preparation).

FIGURES 1-6.—Important specialized South American flea beetles of amphibious amaranths. Dorsal view of female, with more enlarged lateral view of pygidium and propygidium (a) and lateroventral side of abdomen of male (b). 1, *Disonycha argentinensis*. 2, *Agasicles hygrophila*. 3, *A. connexa*. 4, *A. interrogationis*. 5, *A. vittata*. 6, *A. opaca* (lower Amazon River form). In figs. 2a-5a and 2b-5b the external genitalia increase in elaboration, progressing from *A. hygrophila* through *A. vittata*, the vittate species. Also, there is greater elaboration in fasciate *A. opaca* than in *A. hygrophila*.



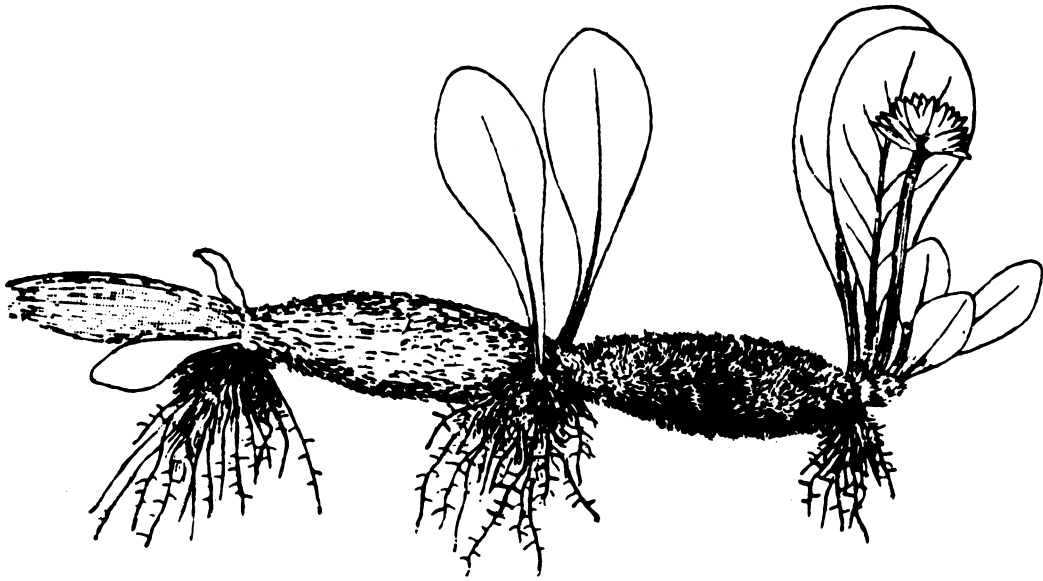
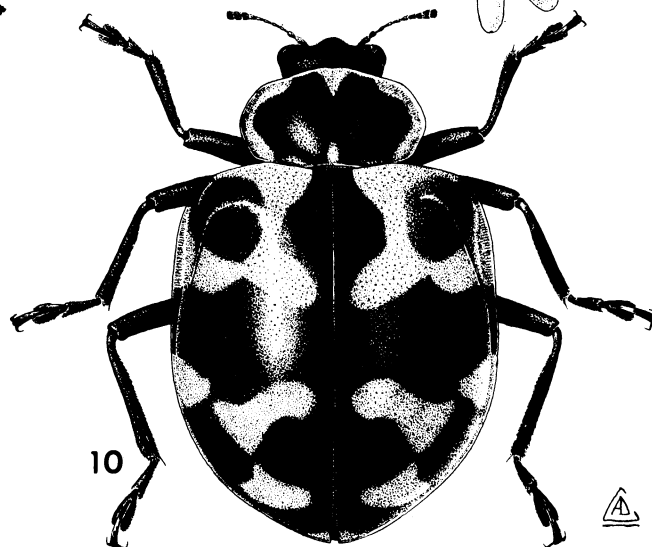
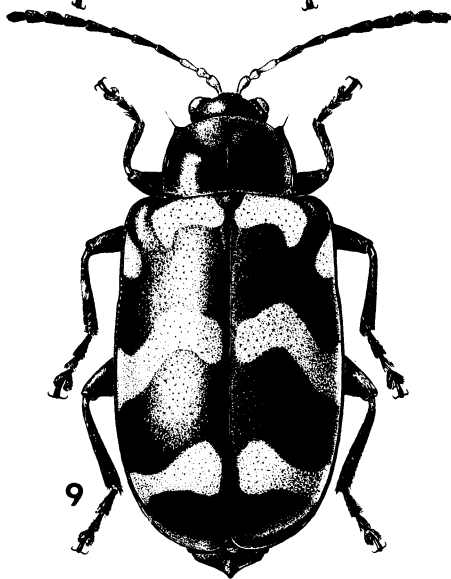
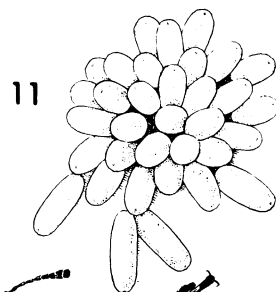
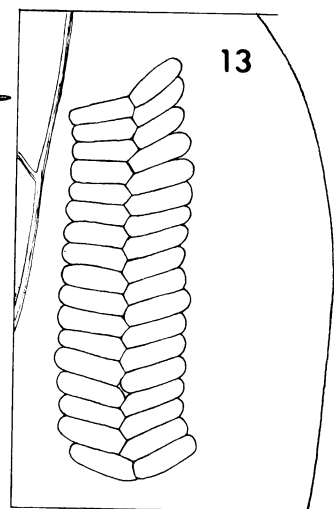
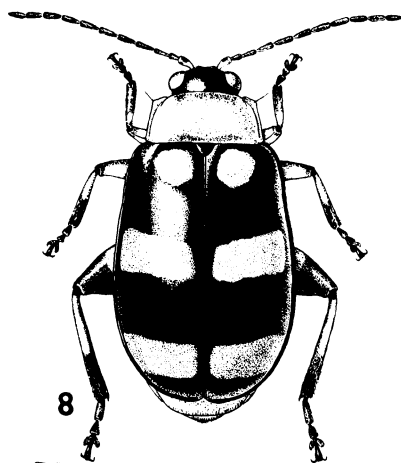
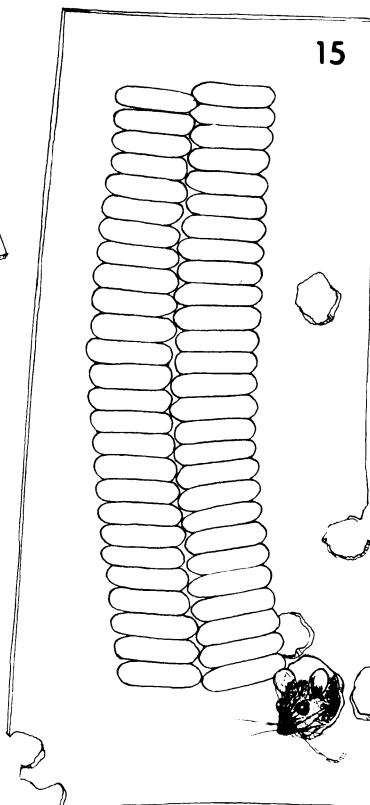
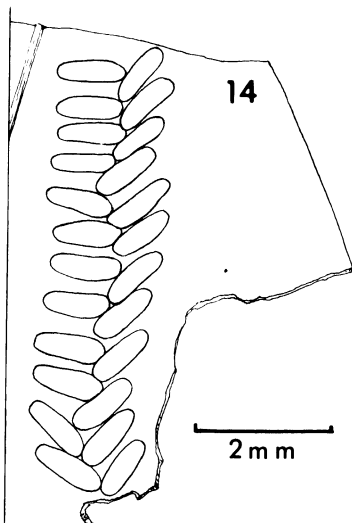
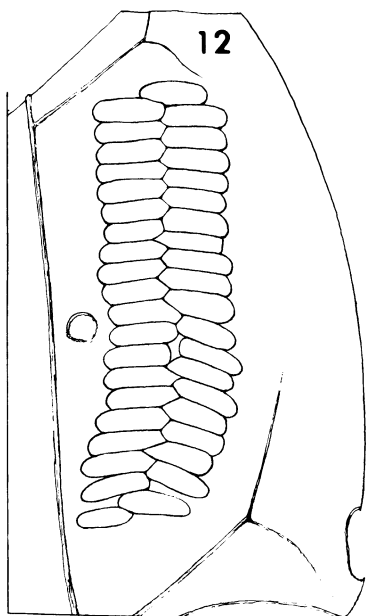
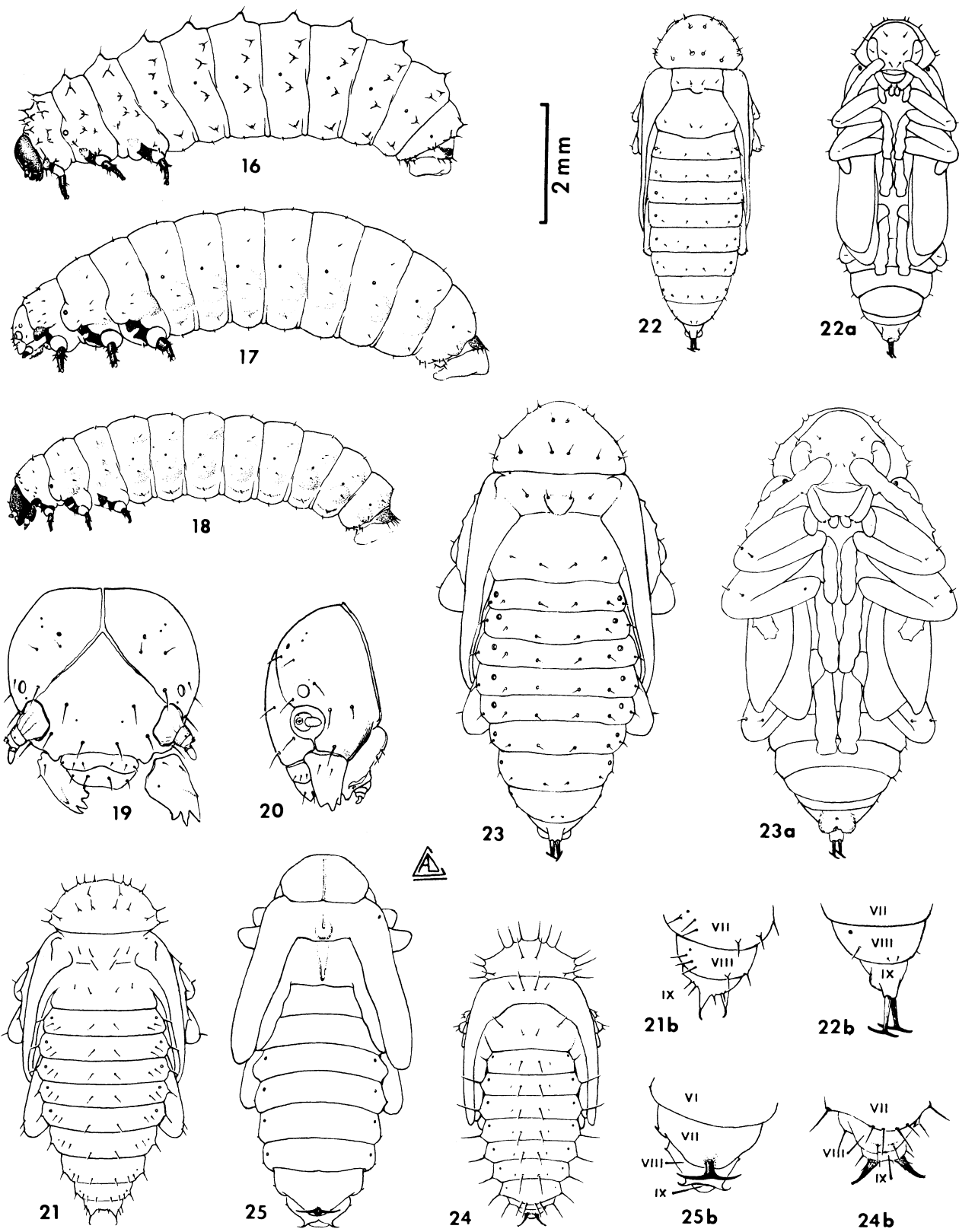
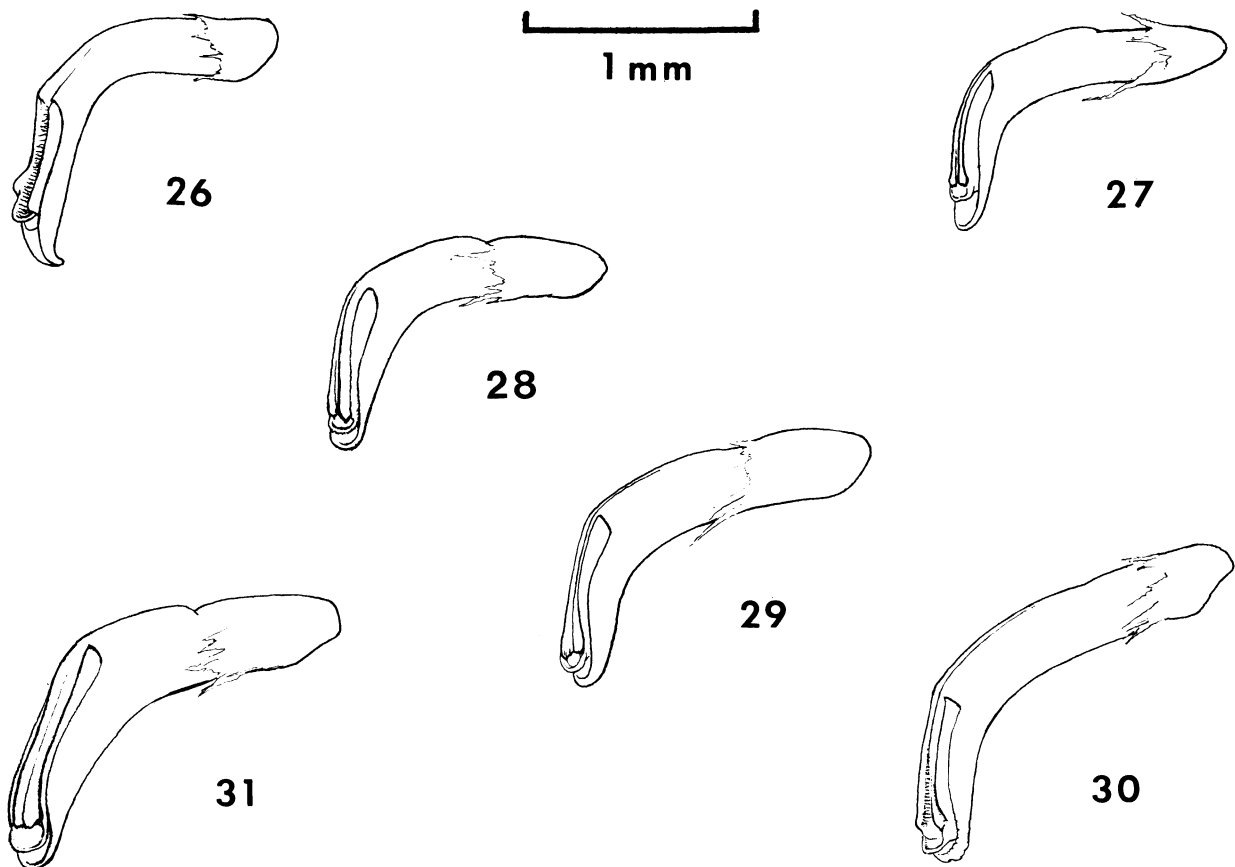


FIGURE 7.—Procumbent floating growth habit of the amphibious amaranth *Alternanthera hassleriana*, from a lagoon along the Paraguay River. Note the pilose surface of the internodes and the extremely short, ascending portion of the stem, less than 10 millimeters long. This plant sometimes forms loosely woven floating expanses over lagoons and backwaters in South America. When competing with stands of *Eichhornia crassipes*, it develops ascending stems like alligatorweed (see frontispiece). (From Chodat 1917.)

FIGURES 8–15.—Two more flea beetles of amphibious amaranths, a coccinellid predator, and disonychine egg masses. 8, One of several species of *Phenrica* that infest amphibious amaranths on terrestrial sites. 9, *Agasicles opaca* (Paraguay River form). 10, *Coleomegilla quadrifasciata*, a probable mimetic model of the fasciate species of *Agasicles* (figs. 6 and 9). 11, Egg mass of *Disonychia argentinensis* in soil at base of stem of host plant. 12–15, Egg masses of *Agasicles* on undersurfaces of leaves of host plant (12, *A. hygrophila*; 13, *A. connexa*; 14, *A. vittata*; 15, *A. opaca*, Paraguay River form).







FIGURES 26–31.—Aedeagi of specialized South American flea beetles of amphibious amaranths. 26, *Disonycha argentinensis*. 27, *Agasicles hygrophila*. 28, *A. connexa*. 29, *A. interrogationis*. 30, *A. vittata*. 31, *A. opaca*.

FIGURES 16–25.—Immature stages of disonychine flea beetles and related Chrysomelidae. 16–18, Related larval flea beetles, advanced third instar, lateral view (16, *Disonycha argentinensis*; 17, *A. opaca*; 18, *A. hygrophila*). 19–20, Head capsule, enlarged to show chaetotaxy, of *Agasicles hygrophila* (19, anterior view; 20, lateral view). 21–25, Various pupal flea beetles and a pupal galerucine. Dorsal view and ventral view (a) of entire insect and more enlarged dorsolateral view (b) of abdominal segments VII, VIII, and IX (21, *Disonycha argentinensis*; 22, *Agasicles hygrophila*; 23, *A. opaca*; 24, *Altica ludoviciana*; 25, *Pyrrhalta* (*Galerucella*) *nymphaea*).

mergence of short duration, but death occurs under prolonged submergence. Moreover, it is completely protected from the ectoparasitic lebiine carabid beetles, which are major enemies of flea beetles that pupate in the soil, including the aquatic *Lysathia* (closely related to *Altica*) species that pupate facultatively in wet soil.

In contrast to an earthen pupal cell that can be formed to fit the contained insect, the stem-internode cavity may be either too large or too small for the pupal *Agasicles*. If it is too large, an insecurely attached pupa could easily fall into a wedged position inside the internode cavity, from which emergence might be impossible. A secure adhesive attaching the prepupal integument to the substrate and a pair of highly modified, T-shaped, giant setae surmounting the abdominal posterior processes of the pupa protect against this eventuality (figs. 22, 22a, 22b, 23, and 23a). To these setae the larval exuviae are inseparably attached.

The anal processes of the *Disonychia* species and other Alticinae that pupate in the soil are armed simply (figs. 21, 21b, 24, and 24b) and insecurely engage the larval exuviae. In the surface-pupating aquatic species of *Lysathia*, the setae surmounting the anal processes are noticeably more developed (fig. 24b), and they cling to the larval exuviae more tightly, but not inseparably as in *Agasicles*. In the aquatic surface-pupating galerucine *Pyrrhalta* (*Galerucella*) *nymphaeae*, evolution has progressed farther and along a different course to produce a remarkable giant T-shaped seta, developed apparently from fusion and great enlargement of the submedian pair of setae of tergite VII instead of the posterior processes of tergite IX (compare fig. 25b with 21b, 22b, and 24b).

If the stem cavity is too small, the prepupal *Agasicles* may enlarge it by chewing away, but not ingesting, the pithy walls. However, this enlargement may result in sufficient weakening to lodge the stem and kill the enclosed insect. Natural selection has, therefore, favored evolution of a slender pupa (compare fig. 22 with 23 and 21) that is more likely to fit inside the stem. Bruch (1906) was first to note this conformation of the pupa.

The dimension most affected by the narrowing process has been the pronotal width. Probably because it is narrower than the pronotum, the head width has been less affected. Also less affected has been the width of the elytra. Elytral width represents maximum body width in the adult (figs. 1–6), but in the pupa the elytra are folded closely against the body. In addition, after ecdysis the elytra are

the last rigid structures to sclerotize in the teneral adult. They remain pliable and conform to the confines of the stem cavity and therefore do not require great reduction in width. Much development of the vitally important wing muscles and reproductive organs occurs after the flea beetle emerges from the stem, thereby filling out the pterothorax and the abdomen, which are embraced by the folded but still pliable elytra.

During or after evolution of the stem internode into the inflated and greatly enlarged form characteristic of *Alternanthera hassleriana* (fig. 7), the flea beetle larva, pupa, and adult became enlarged and broadened to their forms in *Agasicles opaca* (figs. 6, 9, 17, and 23). Elytral markings became fasciate and orange colored in contrast with the ivory markings of the slender vittate species. The form and markings of fasciate *A. opaca* have come to resemble superficially a major predator, *Coleomegilla quadrifasciata* (Coccinellidae) (fig. 10). This ladybird beetle may be a mimetic model because ladybird beetles are thought to be generally distasteful to birds (Hodek 1973). The markings of *Agasicles opaca* are aposematic, judging by Rothschild's (1961) application of the term.

Although they are preyed upon by the same species of coccinellid, the slender vittate species of *Agasicles* show no tendency to mimic their major predator. Instead, they resemble forms of other rather distantly related genera in the Alticinae as well as in the subfamilies Galerucinae and Chrysomelinae. The significance of the resemblance, which seems to be confined to southern South America, is obscure. We have observed no cohabitation of a site by two or more of these forms. But this condition may not be necessary for the existence of mimicry (Hespenheide 1973).

Over the sub-Andean portion of its range, *Agasicles vittata* (fig. 5), a rather large vittate and mostly sylvan species, is entirely dependent on the slender-stemmed *Alternanthera sessilis*. However, along streams in tropical rain forest, where the only natural openings available for colonization are widely separated tree falls, the plant probably grows to full size before the flea beetle can find it. As a result, stem diameters available for prepupal entry may commonly approach those of alligatorweed during the period of initial attack. But drastic reduction in diameter occurs in stems regenerating from heavy *Agasicles* attack. This is also true to a comparable degree in the case of alligatorweed, which is the normal host plant about 800 kilometers downstream. No significant size difference

in the insect was found between the two zones. This is remarkable in view of the mortality in the sub-Andean region, especially of females, from the lodging of small-diameter stems at prepupal entry points.⁹

Except possibly in disturbed situations in the Plains (Llanos) of Mojós, Bolivia, none of the fasciate forms of *Agasicles* mount the massive attacks that the vittate species attain. This difference in suppressive effect is probably because of the hirsute nonascending stem and floating growth habit of *Alternanthera hassleriana*. Little or no regenerative growth of reduced stem diameter that could be restrictive in pupating *Agasicles* occurs. Also, extensive observations in the field show that the fasciate species and their host plant occur typically in insulated lagoons. In contrast, all the vittate species require either cloud cover and rainfall or forest shade for the high humidity (low evaporation rate) needed for massive attacks that result in the reduced stem diameter of regenerative growth.

Affinities Between *Agasicles* and *Disonycha*

Because of their rather slender metathoracic femora, slender prothorax, and general adult body form, species of *Agasicles* were formerly placed in the genus *Systema*. Only recently has a clear relationship between *Agasicles* and *Disonycha* been reported (Selman and Vogt 1971). The affinity is borne out by characteristics of both the adult and immature stages.

The relationship is most evident in similarities in antennal segmentation, in the aedeagi (figs. 26–31), in head capsules, and in metathoracic wing venation of the adults and in the chaetotaxy of the larvae (figs. 16–20). The wings and the larval chaetotaxy of *Agasicles* and *Disonycha* are almost identical.¹⁰ Marked contrasts and discontinuities in these morphological features are found when *Agasicles* and *Disonycha* are compared with less related Alticinae, such as species of *Oedionychus*, *Systema*, and *Altica*, and with species of still more distantly related genera of Galerucinae, such as *Diabrotica* and *Acalymma*. There are no important differences

in larval and pupal chaetotaxy and adult wing venation between *Disonycha* and the closely related genus *Phenrica* Bechyné (1959). In *Agasicles* we have noted no basic departures from *Disonycha* in mating behavior or in the patterns of the feeding processes of adults and larvae.

The egg stages of *Agasicles* and *Disonycha* (figs. 11–15), although distinctive, are very similar, and the first-instar larvae have the same type of egg burster.¹¹ It is vestigial in the second instar and absent in the third. Otherwise, the chaetotaxy of the three larval instars is similar. This is true for various *Disonycha* species and the four species of *Agasicles* that we have studied.

The larvae of *Agasicles* and *Disonycha* are also similar (figs. 16–20). Except for the legs and the ambulatory organ surrounding the anus, the chaetotaxy of the head and body is much less prominent in *Agasicles* than in *Disonycha*. While the prominent tubercles bearing most body setae are somewhat reduced in *Disonycha argentinensis*, as compared with other species of this genus and with species of closely related *Phenrica*, the tubercles have all but disappeared in *Agasicles*, although the setae persist with few exceptions.

This near loss of body tubercles, together with the reduction of most body setae and possibly also some head setae, facilitates stem entry by the prepupal vittate *Agasicles* species and their fitting inside small stems. In contrast, having been freed of the restriction of smaller stem diameters owing to large stems in their host, *Alternanthera hassleriana*, larval and pupal stages of the fasciate *Agasicles* have become quite thickened medially, but the tubercles and most setae of the larval body show no development beyond the atrophied state found in the other species of *Agasicles* (fig. 17). This persistence suggests that the reduction of these larval features is related to the prepupa's drawing its stout body by peristaltic movements through a nearly head-sized entrance hole. Each prepupal *Agasicles* makes such an entrance into the host-plant stem, or, as often occurs in heavy infestations, utilizes a hole made earlier by another prepupa.

The tubercles and their individual prominent setae found in *Disonycha* larvae and prepupae may have important functions associated with daytime resting places in soil and surface litter and in the formation of earthen pupal cells. Such functions are

⁹We found only 3 females (2 of these dead in lodged stems) to 15 males and a dead prepupa.

¹⁰Jolivet (1959) clearly established the basic phylogenetic importance of wing venation in the Alticinae. Böving (1927) and Anderson (1938) provided the basis for our study of larval chaetotaxy.

¹¹Paterson (1930) made earlier studies of the egg burster, using the European chrysomeline *Phaedon* (*Paraphaedon*) *tumidulus*.

unnecessary for the *Agasicles* larvae, which do not hide by day or pupate in soil. Apparently as a protection against high temperatures and low humidity (high evaporation rates), *Disonycha argentinensis* and most other terrestrial disonychines, as larvae and even as adults, are crepuscular to nocturnal, the insects hiding in loose soil and surface litter by day. Since there are no hiding places near the water surface and since the humidity is high there, *Agasicles* adults and larvae do not hide by day.

The larvae of *Disonycha argentinensis* and the *Agasicles* species feed on the stem surface. However, stem entry by *Agasicles* prepupae involves behavioral patterns distinct from stem-surface feeding by *Disonycha*. The biting response of *Agasicles* is not for the purpose of ingestion and may be comparable to the response of prepupal *D. argentinensis* making its way head first into the soil. *Agasicles* prepupae select only stems of their host plants for entry, other plant stems being avoided. This host-plant specificity probably is aimed at the special compartmentalized hollow stem of alligatorweed, a characteristic not found in other aquatic plants that may cohabit with alligatorweed.

This positive, presumably chemotropic response to the host plant apparently has a counterpart in soil-entering prepupal Alticinae. It appears when prepupae of species of *Altica*, *Disonycha*, and *Oedionychus* are confined to rearing containers without soil. They will feed again after a day or more of frustrated searching. Soon afterwards they will enter soil when it is provided.¹² This evidence indicates that the response of the *Agasicles* prepupa to its host plant for stem entry is a carryover from the larval stage. But it is without the response to ingest beyond the foregut. In the case of the soil-entering Alticinae, prepupal feeding is presumably a survival stratagem, and the plant material passes through the enteric tract.

The complex behavior responsible for plugging the head-sized entrance hole by *Agasicles* prepupae also seems to have comparable behavior patterns in the soil-entering alticine prepupae. This comparability becomes evident when prepupae of *Disonycha collata* and *Disonycha pennsylvanica* are confined to rearing containers without soil. Some individuals enter open ends of their hollow-stemmed host plants (in this case alligatorweed and

Polygonum, respectively) and seal off or partition off a cell usually formed by the internode walls and the septa. The seal is composed of plant tissue removed from the stem walls by the mandibles and incorporated with anal or oral exudates or both (Vogt et al., cited in footnote 12). Also, when prepupae of *Disonycha* and *Oedionychus* species enter wet soil, they often form an open-ended cell at the surface. It is sealed by courses of mudlike cement applied successively around the periphery of the open end until it is closed. Apparently, mud is gathered by the anal end of the body and transferred to the forelegs and mouthparts for application. Anal or oral exudates or both are probably incorporated with the mud.

These patterns seem to be consistent with the behavior of the *Agasicles* prepupa, which usually amasses, on the sternum, a small ball of plant tissue by biting several successive courses out of the internode wall. Six or more of the small masses of plant material, applied successively and peripherally, are required to close the head-sized hole (Vogt et al., cited in footnote 12). The mouthparts and forelegs apply the material, as Maddox (1968) reports. An oral exudate seems to be incorporated in the closure, but our observations failed to rule out addition of an anal exudate. For comparison, we note that in various species of the closely related Galerucinae and in some Chrysomelinae, prepupae spin a cocoon from the anus. In the more distantly related Chrysomelidae, a sagrine, *Sagra femorata*, lines its pupal cell with a red to black varnishlike anal exudate. In the Cryptocephalinae and Chlamisinae, the prepupa seals its larval case of fecular material with an anal exudate. In the Clytrinae, soil particles are incorporated with fecular material to form the larval case, which the prepupa seals with a chalky material exuded anally. In these examples of more distantly related Chrysomelidae, the encasing and sealing materials are applied with the mouthparts and forelegs, and this process may entail addition of oral exudates in some cases. In the Curculionidae, some representatives construct cocoons of oral exudates (*Hypera*), while others utilize anal exudates (*Odontopus*). Several genera of leaf-mining Agrilinae (Buprestidae) spin cocoons from the anus, and some of these are remarkably elaborate. Even in the aberrant family Brachypsectridae, the prepupa spins a cocoon from the anus.¹³

The pupae of the *Agasicles* species and *Disonycha argentinensis* differ markedly. The re-

¹²G. B. Vogt, P. C. Quimby, Jr., and S. H. Kay, "Field Studies of Flea Beetles, Host Plants, and Lebiine Predator Parasites in the Southern United States" (in preparation).

¹³G. B. Vogt, unpublished notes.

markable T-shaped terminal abdominal setae of *Agasicles* have already been discussed. In addition, the *Agasicles* pupa has lost two pairs of setae from the disk of the pronotum and a pair of lateral setae from each abdominal segment (figs. 21–23). We believe this loss is a result of the restrictive effects of the slender host-plant stem upon the *Agasicles* pupa. Furthermore, the pupa of *Disonycha argentinensis* shows no transitional features between other species of its genus and *Agasicles*. Pupae within the genus *Agasicles* have consistent chaetotaxy.

Biogeography of Flea Beetles and Their Host Plants

The four amphibious amaranths and the related halophyte of coastal beaches, *Philoxerus*, are distributed as shown in figures 32 and 33. Excepting *Philoxerus*, the plants occur principally in alluvial lands. The range of *Alternanthera hassleriana* is subtropical to tropical, and is contained within the limits of the farther ranging alligatorweed. Alligatorweed is centered principally in subtropical to temperate southern South America, with additional important centers along the Brazilian east coast, in the upper and middle Amazon basin, and in northern South America from Belém to Trinidad.

Alternanthera sessilis is tropicopolitan and, in South America, it occurs on both sides of the Andes. Although it overlaps the range of alligatorweed, most importantly it occurs as the sole amphibious amaranth in the upper Amazon River, adjacent to and somewhat within the Andean ranges. *A. sessilis* is also a host plant of *Agasicles interrogationis* and *A. connexa* along the narrow littoral of Brazil, where our findings show alligatorweed to be the major host plant. While *Alternanthera sessilis* tends to be a sylvan species, we have no evidence of its occurrence in South America outside areas under some degree of human disturbance. It seems most at home in the eastern Andean foothills. As already stated, Pedersen (cited in footnote 6) considers the affinities of *A. sessilis* to be with species of Southeast Asia rather than those of the New World.

Alternanthera obovata, the probable North American counterpart of alligatorweed, ranges from Honduras northward to within 400 kilometers of Brownsville, Tex. Apparently no specialized flea beetles have evolved on this plant because of the limited area and diversity of the alluvial lands included in its range. The Western-Hemisphere-wide

coastal halophytes, *Philoxerus* species, also apparently support no flea beetles, although they are hosts of one of the important specialized insects of amphibious amaranths, the phycitine moth, *Vogtia malloi*. However, along the beaches of the Gulf of Mexico, *P. vermicularis* and several Chenopodiaceae are normal hosts of a galericine, *Eryne-phala maritima*.

Figures 34 and 35 show the distribution of the five species of *Agasicles*, *Disonycha argentinensis*, and the species of the closely related genus *Phenrica* that are known to attack amphibious amaranths. Table 1 gives known host plants of these and other *Alternanthera*-oriented flea beetles. *Agasicles* is limited to the humid, mostly alluvial regions east of the Andes. We have no record of this genus north of the Equator. All species, as known presently, are allopatric except the vittate species *A. hygrophila* and the fasciate Paraguay River form of *A. opaca*. *D. argentinensis* is mostly coextensive with *Agasicles* except that it is absent from all but the southernmost reaches of the Amazon River basin. It also extends beyond the range of *Agasicles* into oases of the dry regions east of the Andes and at São Luis, Maranhão State, Brazil (Costa Lima 1954 and Blake 1955). At most of these localities, alligatorweed is known to occur, but three alternative host plants are now known for *Disonycha argentinensis* that are not necessarily confined to alluvial lands. *Alternanthera paronychioides* and *A. pungens*, widespread over much of southern South America east of the Andes, are host plants near Santa Cruz, Bolivia, and Corumbá, Mato Grosso, Brazil. *Alternanthera kurzii*, widespread in the Chaco and adjacent regions (Pedersen 1967), is a host plant in just a few localities between the Bermejo River and Arroya Empedrado along the Paraná and Paraguay Rivers. *D. argentinensis* shares this host plant with *Phenrica*, which is the only genus of flea beetle we found on this host north of the Bermejo River (Vogt and Cordo 1976).

Phenrica ranges over much of tropical North America, as well as over all of humid South America except the temperate southern areas. The void in this distribution includes the important region of the lower Paraná River and the Río de la Plata, which is the present stronghold of both *D. argentinensis* and *A. hygrophila*. *Phenrica* is a large complex of closely related stenophagous species for which we have yet to work out satisfactory identifications. The reader must bear in mind that, as cited in table 1, the *Phenrica* of *Amaranthus*, of *Iresine*,

(Continued on page 22.)

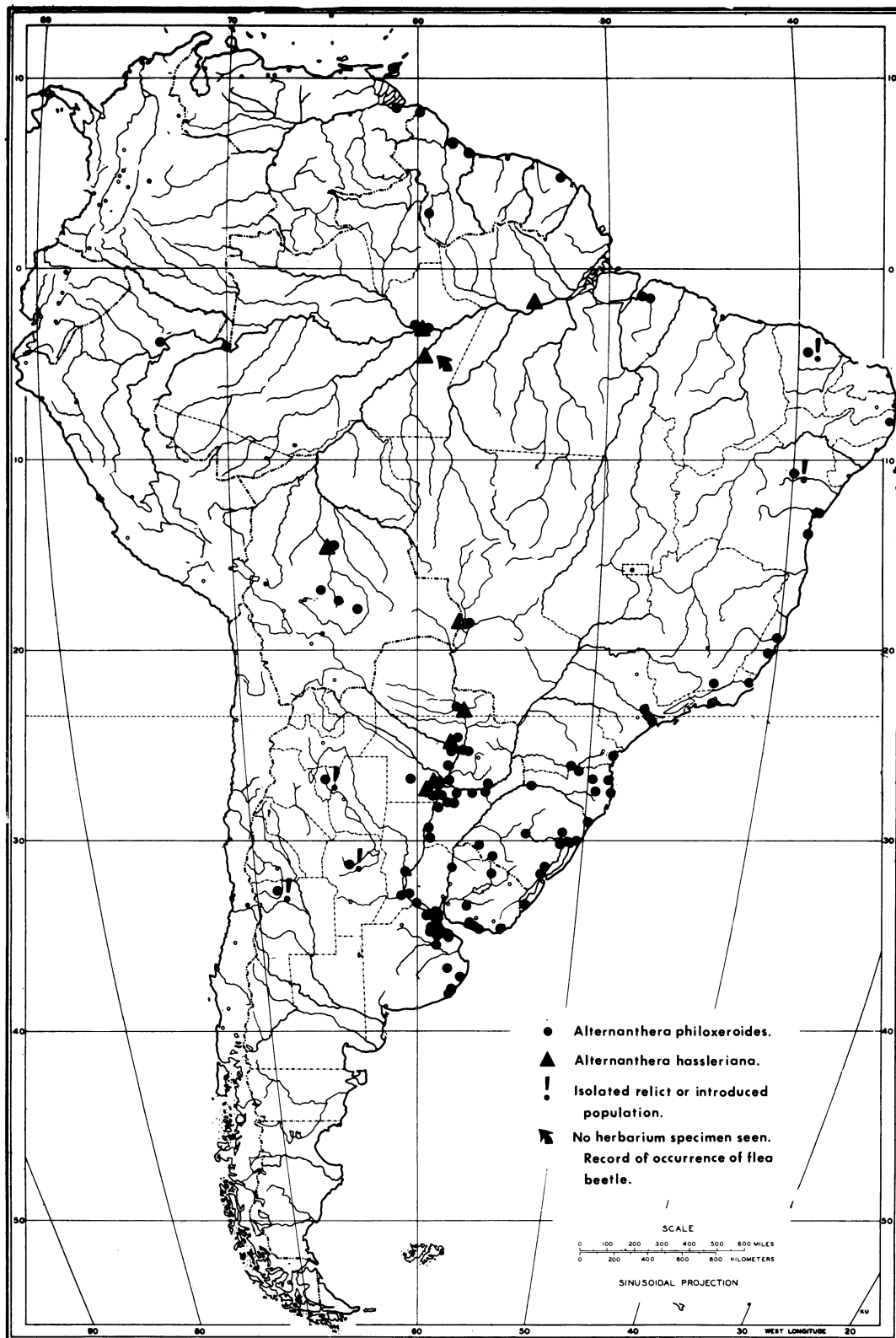


FIGURE 32.—South American distribution of alligatorweed and *Alternanthera hassleriana*. The records are from the Instituto Darwinión, U.S. National Herbarium, and other herbaria and from Foster (1948), Smith and Downs (1972), and Vogt et al., cited in footnote 8. (Goode Base Map copyright by The University of Chicago Department of Geography.)

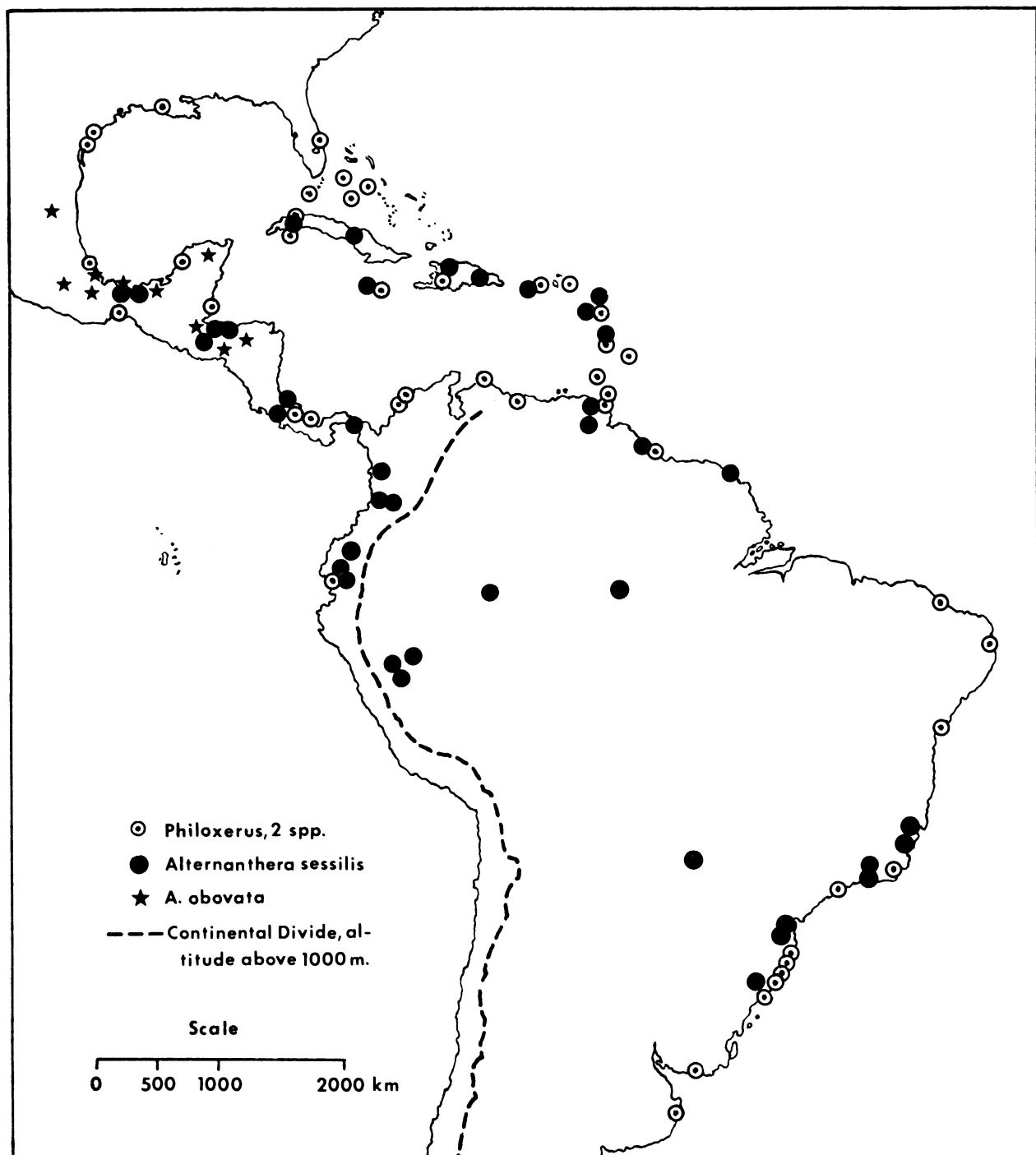


FIGURE 33.—Western Hemisphere distribution of the amphibious amaranths *Alternanthera sessilis* and *A. obovata* and of the combined halophytic amaranths *Philoxerus vermicularis* and *P. portulacoides*. These records are from the U.S. National Herbarium and Vogt et al., cited in footnote 8.

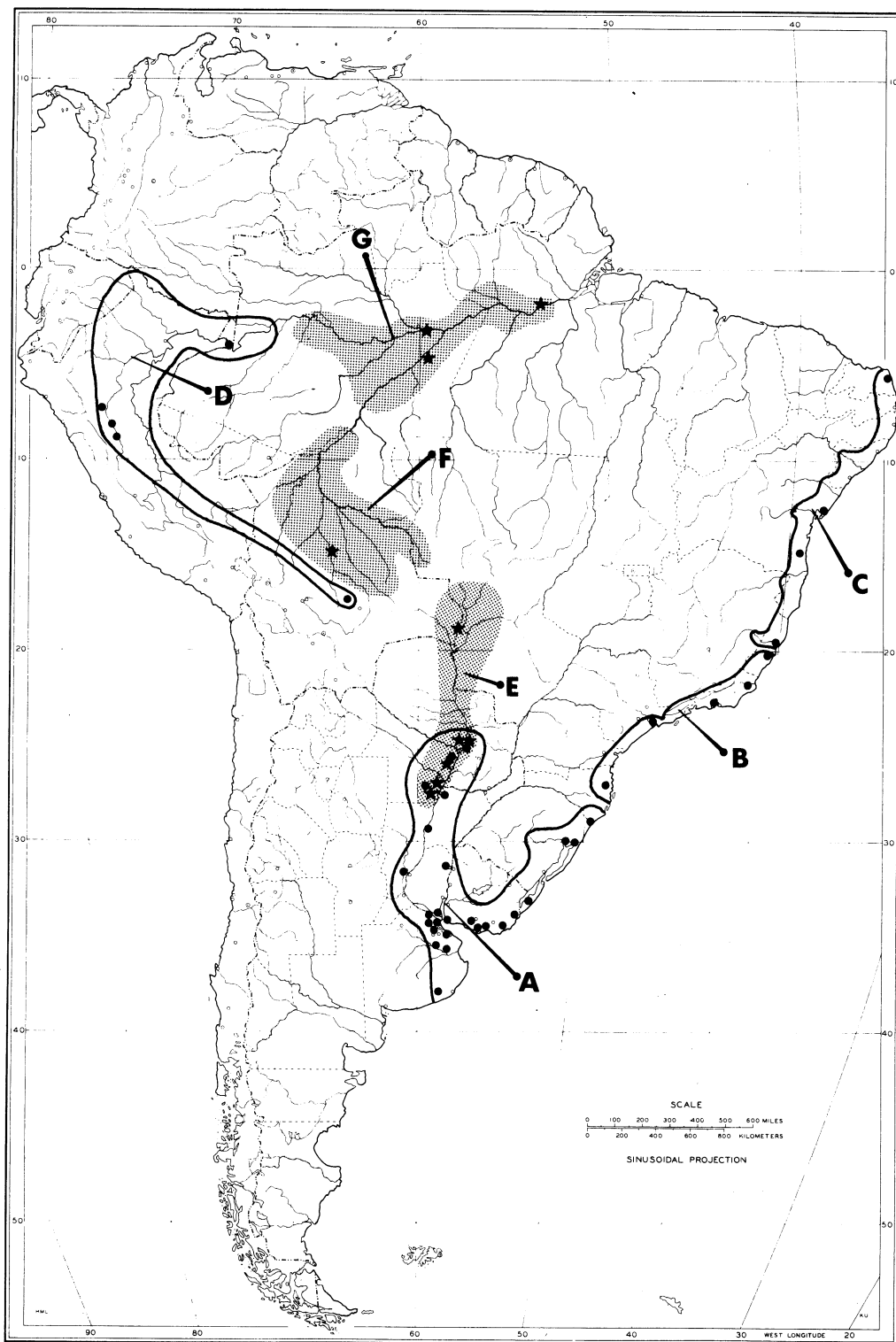


FIGURE 34.—South American distribution of *Agasicles* species. Vittate species (unshaded): A, *A. hygrophila*. B, *A. connexa*. C, *A. interrogationis*. D, *A. vittata*. Fasciate *A. opaca* (shaded): E, Paraguay River form. F, Plains of Mojós form. G, Lower Amazon form. In this study, we sampled and observed *Agasicles* at 44 of the 50 localities shown. Of the remaining six records, four (Natal, Ilheus, Santos, and Santa Tomé) are from the University of Paraná collections and from the U.S. National Museum of Natural History. Two (Borba and Río Mixiollo) are cited in Selman and Vogt (1971). (Goode Base Map copyright by The University of Chicago Department of Geography.)

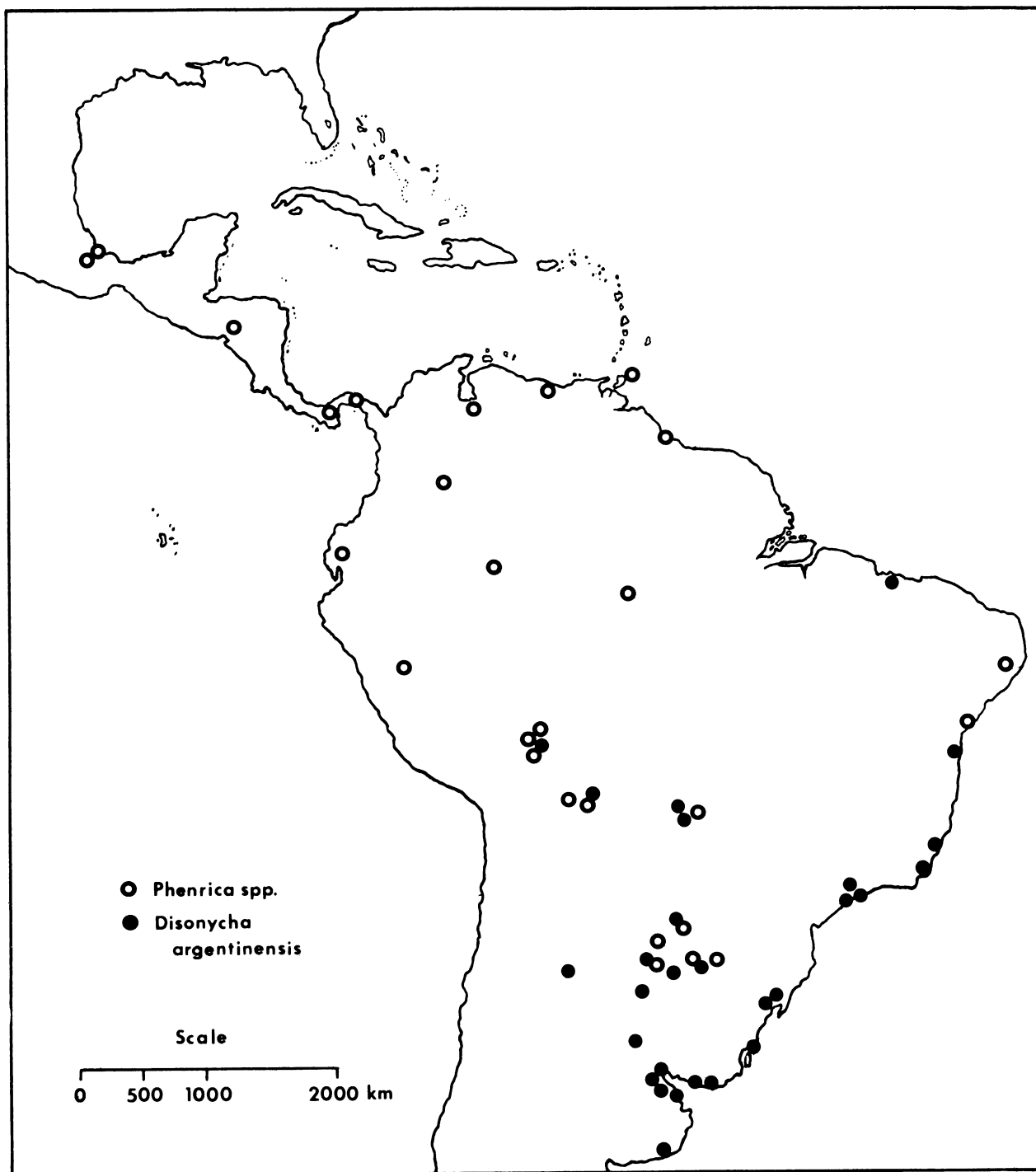


FIGURE 35.—Distribution of *Disonycha argentinensis* and *Phenrica* species, known herbivores of amphibious amaranths growing on terrestrial sites. These records are from the U.S. National Museum of Natural History, the Carnegie Museum, Costa Lima (1954), Blake (1955), and Vogt et al., cited in footnotes 8 and 12.

Table 1.—Known host plants of *Alternanthera*-oriented disonychine flea beetles (*Disonycha*, *Phenrica*, and *Agasicles*) and *D. conjuncta*, one of many non-*Alternanthera*-oriented species

Flea beetle and distribution	<i>Stellaria media</i>	<i>Trianthema portulacastrum</i>	<i>Spinacia oleracea</i>	<i>Beta vulgaris</i>	<i>Chenopodium album</i>	<i>Iresine diffusa</i>	<i>Amaranthus</i> spp.	<i>Chamissoa</i> spp.	<i>Cyathula</i> spp.	<i>Alternanthera</i>									
										<i>ficoidea</i>	<i>halimifolia</i>	<i>obovata</i>	<i>philoxeroides</i>	<i>hassleriana</i>	<i>sessilis</i>	<i>kurzii</i>	<i>paronychioides</i>	<i>pungens</i>	Unidentified spp.
<i>D. xanthomelas</i> :																			
Northern U.S. and Canada ...	+		+	+	+								+						
Southern U.S.			+	+	+	+	+												
<i>D. collata</i> :																			
Southern U.S.		+	+	+		+	+						+					+	
Mexico						+						+			+				
Colombia															+				
<i>D. camposi</i> : Ecuador and Peru ...							+				+				+				+
<i>D. eximia</i> :																			
Panama										+					+				
Trinidad, West Indies													+						
<i>D. glabrata</i> :																			
North America							+	+					+						
South America							+												
<i>D. proluxa</i>							+												
<i>D. argentinensis</i>													+	+		+	+	+	
<i>D. conjuncta</i>						+													
<i>Phenrica</i> spp.: Mexico; Central and South America						+			+	+			+	+	+	+		+	+
<i>A. opaca</i> :																			
Lower Amazon River form ...													+	+					
Plains of Mojós form														+					
Paraguay River form													+	+					
<i>A. vittata</i>													+		+				
<i>A. hygrophila</i>													+						
<i>A. connexa</i>													+		+				
<i>A. interrogationis</i>													+		+				

¹Adult orientation only; on this host plant, eggs hatch, but larvae do not develop.

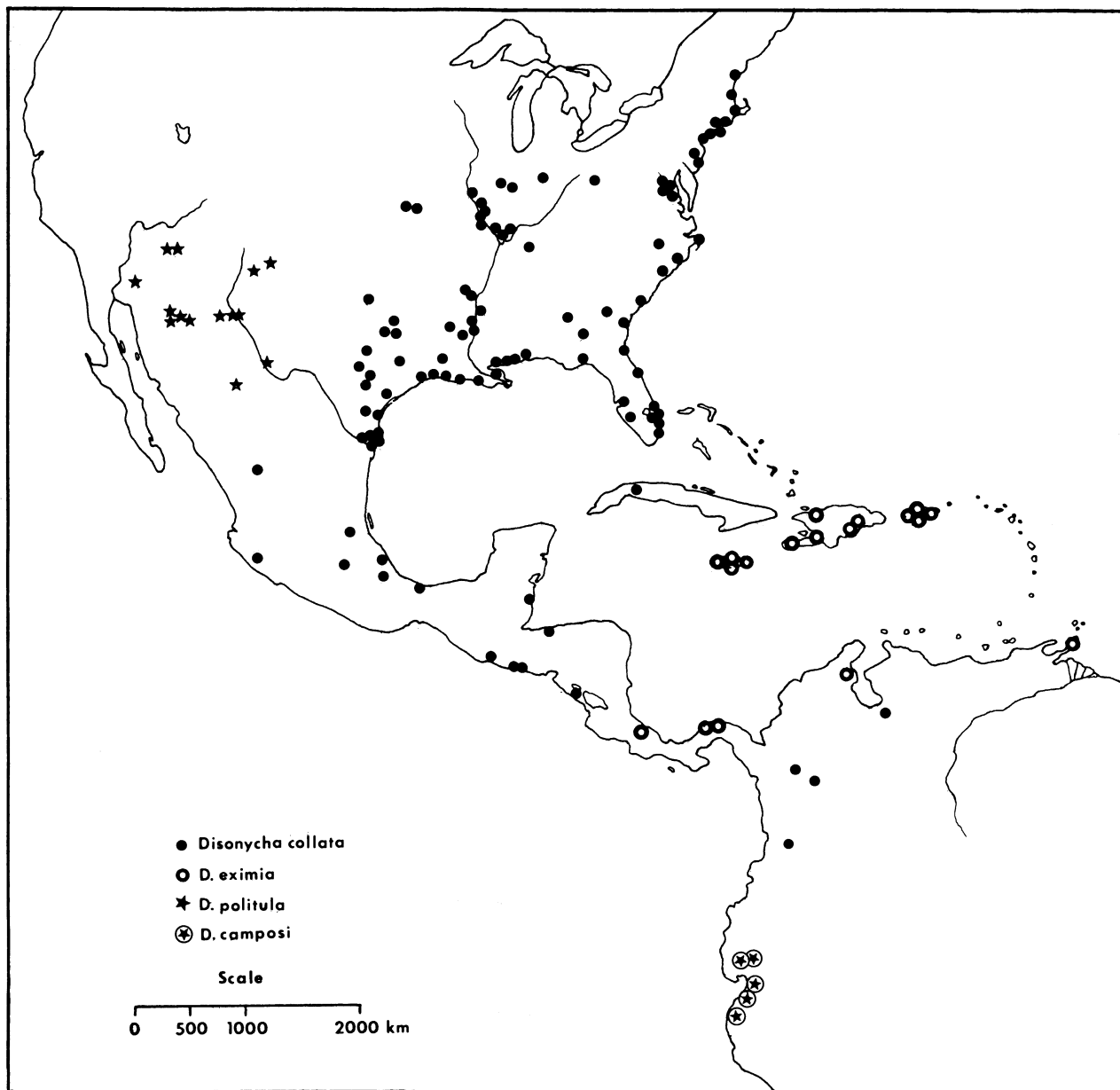


FIGURE 36.—Distribution of four closely related indigenous North American and South American species of *Disonycha*. *D. collata*, *D. eximia*, and *D. camposi* infest terrestrial plants of amphibious amaranths, while *D. politula* is a related species of semidesert habitats. Closer study may reveal that *D. collata* as represented here is actually either a superspecies or a polytypic species composed of closely related forms. Records are from the U.S. National Museum of Natural History, Blake (1933), Brimley (1938), Fattig (1948), Wilcox (1954), Kirk (1969 and 1970), Balsbaugh and Hayes (1972) and Vogt et al. as cited in footnotes 8 and 12.

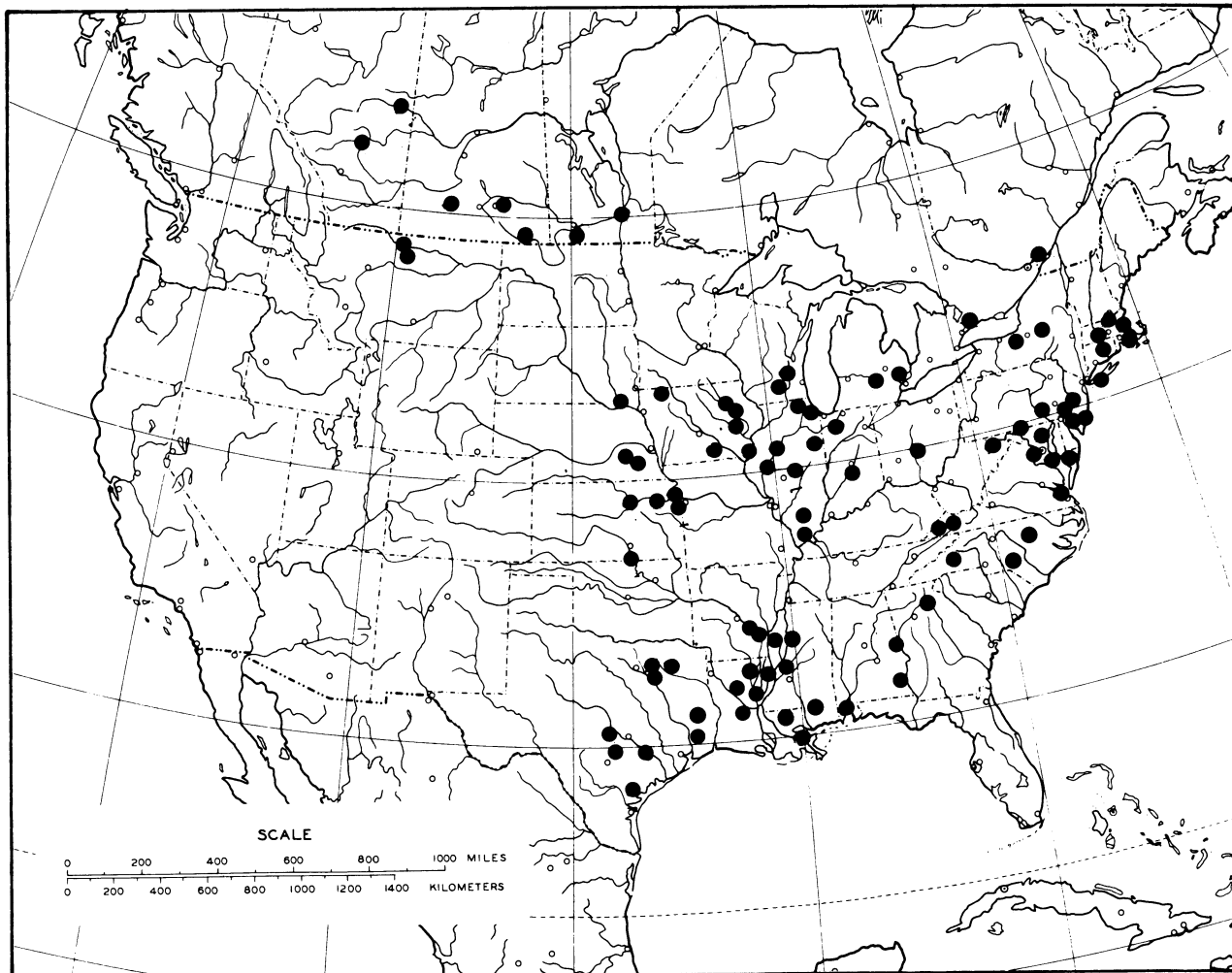


FIGURE 37.—Distribution of North American *Disonycha xanthomelas*. Unlike *D. collata*, this species approaches but does not reach the seacoast anywhere in its range along the Gulf of Mexico. Records are from the U.S. National Museum of Natural History, Blake (1933), Brimley (1938), Fattig (1948), Wilcox (1954), Kirk (1969 and 1970), Balsbaugh and Hayes (1972), and Vogt et al., cited in footnotes 8 and 12. (Goode Base Map copyright by The University of Chicago Department of Geography.)

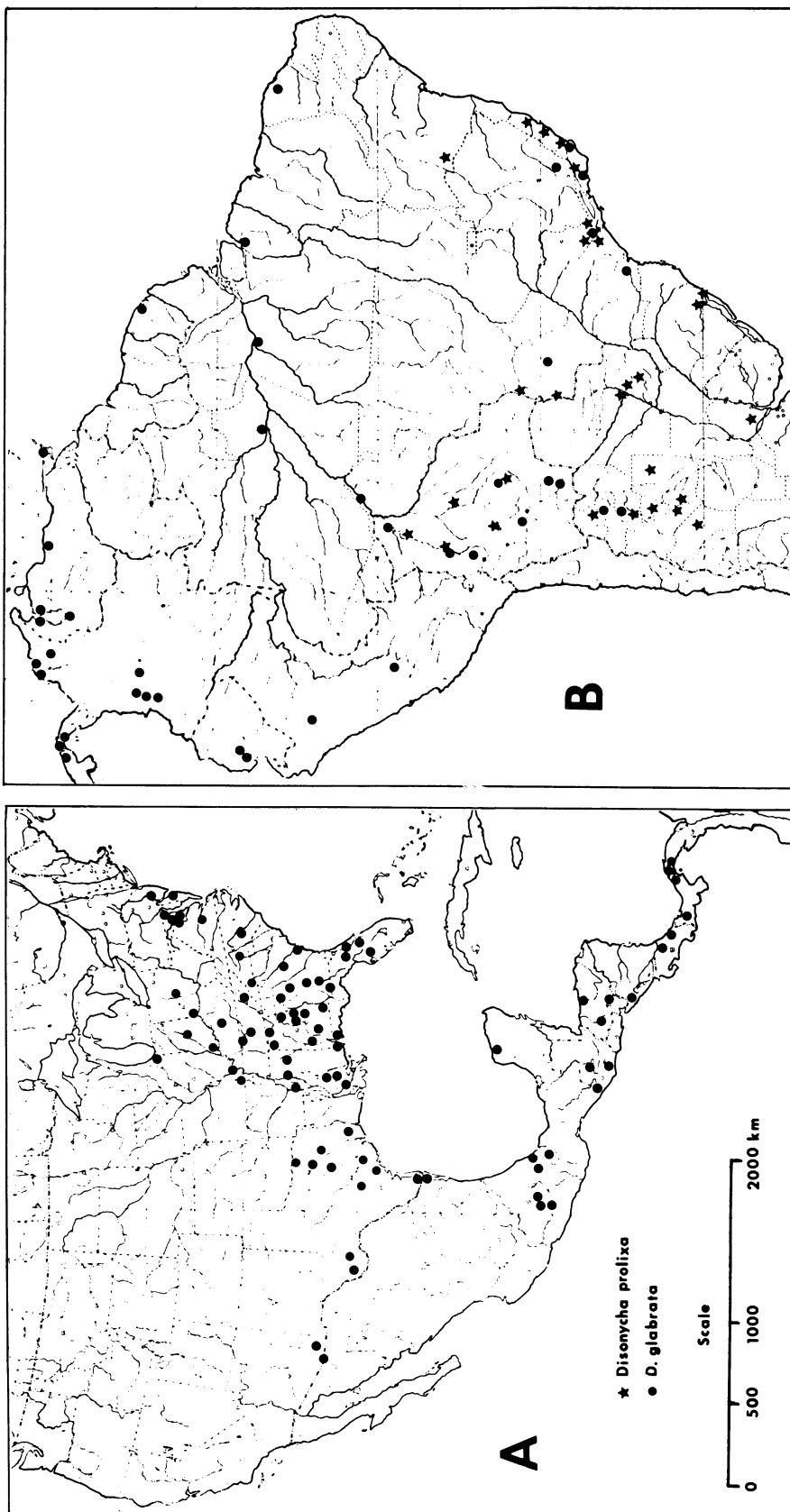


FIGURE 38.—North American (A) and South American (B) distribution of *Disonychia glabrata* and closely related *D. proliza*. Records are from the U.S. National Museum of Natural History, Blake (1933, 1955), Brimley (1938), Fattig (1948), Wilcox (1954), Costa Lima (1954), Kirk (1969, 1970), Balsbaugh and Hoeyes (1972), and Vogt et al., as cited in footnotes 8 and 12. (Goode Base Map copyright by The University of Chicago Department of Geography.)

of *Cyathula*, and of *Alternanthera* are distinct from one another. Also, within those injurious to *Alternanthera* there is a complex of both sympatric and allopatric *Phenrica* species.

The largest *Agasicles* flea beetles are the forms of fasciate *A. opaca*. They are coextensive with the range of their host plant, *Alternanthera hassleriana*, the largest-stemmed amphibious amaranth. However, the smallest species of *Agasicles*, *A. hygrophila*, does not occur within the range of *Alternanthera sessilis*, the amphibious amaranth having the most slender stems. (Compare fig. 34 with figs. 32 and 33.) From Asunción to Resistencia, Province of Chaco, Argentina, the Paraguay River form of *Agasicles opaca* occasionally infests alligatorweed in disturbed situations. We also found it exploiting alligatorweed below Manaus in the lower Amazon.

Figures 36 and 37 show the distribution of five *Disonycha* species indigenous to North America and northern South America. Four infest amphibious amaranths, and the fifth, *D. politula*, is a related species of semidesert habitats. Table 1 gives host plants of the known *Alternanthera*-oriented flea beetles. In Panama, *D. eximia* develops on terrestrial plants of *Alternanthera sessilis* and on the mesophyte *Alternanthera ficoidea*. It also attacks alligatorweed in Trinidad, West Indies.

In the Southern United States, *Disonycha collata* develops in nature on various Centrospermae, as follows: *Trianthema portulacastrum* (Aizoaceae); *Chenopodium album*, spinach, and beet (Chenopodiaceae); and *Acnida*, *Amaranthus*, *Iresine diffusa*, *Alternanthera pungens*,¹⁴ and alligatorweed (Amaranthaceae) (Vogt et al., cited in footnote 12). Blake (1933) also lists *Portulaca* (Portulacaceae), chickweed (Caryophyllaceae), and lettuce (Compositae). Our studies show that chickweed, *Stellaria media*, may be a host when it grows as a summer annual in cold latitudes, but not when it grows as a winter annual in warm latitudes. In Mexico, *Disonycha collata* infests the amphibious amaranth *Alternanthera obovata* (fig. 33) in low-lying terrestrial situations and the mesophyte *Iresine diffusa* in the uplands. In Colombia, a geographical form of *D. collata* develops on terrestrial *Alternanthera sessilis* (Vogt et al., cited in footnote 8). West of the Andes in Ecuador and Peru, a closely related species, *D. camposi*, develops on *Amaranthus*, *Alternanthera halimifolia*,

Alternanthera sessilis, and an unidentified *Alternanthera* species.¹⁵ In tropical to subtropical forest east of the Andes and in Panama, one or more fasciate *Phenrica* species attack the Western-Hemisphere-wide *Iresine diffusa*. Further south and into the temperate region, a vittate species, *Disonycha conjuncta*, is specific on this host plant, with no trace of *D. argentinensis* being found on it anywhere. Somewhat similarly, east of the Andes, *Amaranthus* supports two to three vittate species of *Disonycha*, except in the upper Amazon Basin, where species of *Phenrica* replace them. Again no trace of *D. argentinensis* is found on this plant anywhere (Vogt and Cordo 1976).

From the distribution patterns and host-plant relations just given, we conclude that the ancestral forms of *Disonycha collata* and its vicarious forms, *D. eximia* and *D. camposi*, probably invaded South America no earlier than the late Pliocene. Furthermore, because their distribution is limited to the northwestern fringes of South America, the invasion may have occurred after the final major uplift of the northern Andes. Vanzolini and Williams (1970), Haffer (1974), and Raven and Axelrod (1975) consider that massive immigration of vertebrates from North America occurred in the late Pliocene after the Middle American land bridge came into existence. In addition, Haffer (1974) states, "The exchange of northern and southern nonforest faunas through northwestern Colombia may never again have been as intensive as toward the end of the Pliocene prior to the final uplift of the [northern] Andes and prior to the expansion of tropical lowland forests." *Disonycha collata* and its vicarious forms may be considered as mostly nonforest faunal elements.

The indigenous North American *Disonycha xanthomelas*, together with closely related *D. collata*, has been found developing on terrestrial alligatorweed, *Amaranthus* (including *Acnida*) species, *Iresine diffusa*, *Chenopodium album*, beet, and spinach at various locations in the Southern United States (Quimby and Vogt 1974 and Vogt et al., cited in footnote 12). Blake (1933) includes chickweed, *Stellaria media*, as a host plant of *D. xanthomelas*. As with *D. collata*, our studies indicate that chickweed is a host in cold climates where it grows as a summer annual, but not in warm climates where it is a winter annual. In contrast with

¹⁴*Alternanthera pungens* (not *A. repens*) is established as an exotic species in the Southern United States (Pedersen 1967).

¹⁵G. B. Vogt and H. A. Cordo, "Field Studies of Flea Beetles, Host Plants, and Lebiine Predator Parasites in South America" (in preparation).

D. collata, *D. xanthomelas* does not occur on *Trianthema portulacastrum*, nor will it develop on this host plant in the laboratory. *D. xanthomelas* is widespread in Canada and approaches but does not reach the Gulf of Mexico as far south as Victoria, Tex. (fig. 37). We have not found *Disonycha triangularis*, which is closely related to *D. xanthomelas*, in the Southern United States (Vogt et al., cited in footnote 12). They have largely overlapping ranges except that *D. triangularis* trends farther west southwardly. Also, this species seems to be more oriented to the Chenopodiaceae, although Blake (1933) lists *Amaranthus* species as host plants.

The transference of *Disonycha collata* and *D. xanthomelas*, two indigenous North American flea beetles, to alligatorweed in the Southern United States indicates chemical similarity of plants and may be important evidence of an affinity between *Disonycha* and *Agasicles*. Also, we have found *Disonycha glabrata* adults feeding on alligatorweed at isolated but widespread localities in the Southern United States. This is either a transitional transference or a vestige of an old orientation to *Alternanthera* because this flea beetle does not complete its development on this plant (Vogt et al., cited in footnote 12). In South America, *D. glabrata* has not been observed to attack alligatorweed or any other species of *Alternanthera* (Vogt and Cordo 1976). This discontinuity in a region rich in *Alternanthera* species could be a manifestation of an old character displacement involving host ranges of ancestral forms of *Disonycha glabrata*, *D. argentinensis*, and possibly *Phenrica* species (see p. 38). However, all of our records of *D. glabrata* on alligatorweed in the Southern United States are of springtime occurrences. Because that region has been extensively surveyed at all seasons, the occurrences probably represent host-plant responses of flea beetles enroute from hibernation to their normal host plants, *Amaranthus* (including *A. nida*) species. Only late summer and fall observations were made in South America. Therefore, these very extensive observations are not strictly comparable. But if the imperfect orientation of *Disonycha glabrata* to alligatorweed is a vestige of an old orientation to *Alternanthera*, this vittate species could be the closest intrageneric relative of the vittate *D. argentinensis*.

Unlike *Disonycha collata* and *D. xanthomelas*, *D. glabrata* ranges widely over South America and overlaps much of the range of *D. argentinensis* (Costa Lima 1954 and Blake 1955) (figs. 36–38). Both *Disonycha glabrata* (together with closely re-

lated *D. prolixa*) and *D. argentinensis* are attacked by specific, highly mimetic, vittate species of ectoparasitic *Lebia* in South America (Vogt and Cordo, cited in footnote 15), but as presently known, no vittate species of *Lebia* attacks *D. glabrata* in North America (Vogt et al., cited in footnote 12). This diverse information may indicate that *D. glabrata* has an older history in South America than in North America.

While the perfect transference of the North American *Disonycha xanthomelas* and *D. collata* and the West Indian *D. eximia* may indicate affinity with *D. argentinensis*, none of them overlap the indigenous South American range of alligatorweed in Recent time except *D. eximia*, which attacks this plant in Trinidad, West Indies (figs. 32 and 36). Possibly the Andes Mountains and the dry climate across northern South America have been effective barriers to their southward dispersal. We have no evidence of their ancestral forms being involved in the speciation that led to archetypal populations of *Disonycha argentinensis*. Possibly some of the same factors limiting the southward advance of *D. collata* and *D. eximia* have limited the northern advance of alligatorweed. On the other hand, we suspect that the ecologically similar vittate *Disonycha glabrata* and the ecologically similar fasciate *Phenrica* species passed through the northern Andes prior to the final uplift because of their distribution on both sides of the Andes and far to the south into Argentina, as well as far into North America. Also, an old South American history for *Disonycha glabrata* may be indicated by the comparability between the following disonychine flea beetles and their mimetic and nonmimetic predators: vittate *D. glabrata* and *D. prolixa* and their vittate *Lebia* predator; *D. argentinensis* and its vittate *Lebia* predator; fasciate *Phenrica* and their fasciate *Lebia* predators; the vittate *Agasicles* and their nonmimetic *Coleomegilla* predator; and the fasciate *Agasicles* and their mimetic *Coleomegilla* predator.

Sixty to sixty-three insect species were found to feed and develop on amphibious amaranths in South America (Vogt et al., cited in footnote 8). Of these insects, 11 species are narrowly host specific and are listed in table 2. Their occurrence with amphibious amaranths, especially alligatorweed and its closest relative, is consistent and widespread. The more numerous, less specialized to generalized species, with the possible exception of *Herpetogramma bipunctalis* (Pyraustidae), occur irregularly or only locally. We interpret these patterns

Table 2.—Characteristics of the genera that include the 11 recognized, most highly specialized species oriented to the amphibious amaranths in South America

Genus (family)	Feeding range of genus	No. species in genus	Eleven alligator-weed-specialized species	No. of localities where species found	Penetration ¹ of alligatorweed ² range (percent of area including 105 alligatorweed localities)	
					Species	Genus
<i>Amynothrips</i> (Phlaeothripidae)	Stenophagous	1	<i>A. andersoni</i>	31	81.6	81.6
<i>Vogtia</i> (Pyralidae)	do	1	<i>V. malloi</i>	34	81.4	81.4
			<i>A. hygrophila</i>	26	18.3	
			<i>A. connera</i>	5	4.0	
			<i>A. interrogatiohis</i>	4	6.1	
			<i>A. vittata</i>	5	12.8	
<i>Agasicles</i> (Chrysomelidae)	do	5	<i>A. opaca</i> :			374.1
			Paraguay River form	6	9.4	
			Plains of Mojos form	1	13.0	
			Lower Amazon form	4	13.1	
<i>Disonychia</i> (Chrysomelidae)	Polyphagous	100+	<i>D. argentinensis</i>	28	47.4	47.4
<i>Melanagromyza</i> (Agromyzidae)	do	100+	<i>M. alternanthera</i>	18	82.4	482.4
			<i>M. marrellii</i>	8	19.2	
<i>Ophiomyia</i> (Agromyzidae)	do	50+	<i>O. buscki</i>	7	23.1	23.1

¹Based on estimated areas that include the 105 localities plotted on fig. 32 (alligatorweed, relict localities excepted) and the localities plotted on figs. 34 (*Agasicles* spp.) and 35 (*Disonychia argentinensis*). We estimate that 39.0 percent of the extrapolated area of alligatorweed range remains unexplored for biotic agents. An estimated 35 percent of the range of *Agasicles vittata* extends beyond the range of alligatorweed because of a corresponding extension in the range of *Alternanthera sessilis*. Also, the range of *Vogtia malloi* extends beyond the range of alligatorweed into the dry regions of northeastern Brazil, where *Philoxerus* serves as a host plant. Distribution maps for *Vogtia*, *Amynothrips*, and the Agromyzidae will be published in a later bulletin (Vogt et al., cited in text footnote 8). Map areas were obtained from cutout patterns with a portable Lambda LJ-3000 area meter.

²The closest relative of alligatorweed, *Alternanthera hassleriana*, is included as shown on fig. 32.

³A value of 2.6 percent has been subtracted from this total to compensate for the overlapping ranges of *Agasicles hygrophila* and the Paraguay River form of *A. opaca*.

⁴The penetration of *Melanagromyza marrellii* is not added because its range is completely overlapped by that of *M. alternanthera*.

of occurrence as being consistent with the conclusions of Connell (1961) and McNaughton and Wolf (1970) that different species specialize with respect to different environmental parameters. In phytophagous species, those that specialize on host-plant species become more efficient exploiters of those species and therefore more dominant in occurrence. At the same time, they may force less specialized species (with respect to host species) into peripheral specializations which may result in their uneven occurrence and low level of fidelity with respect to the specialist's host spectrum.

From table 2 we see that four of the specialized insects, *Disonycha argentinensis* and three species in the family Agromyzidae, belong to large, polyphagous genera. In contrast, two of the remaining eight species belong to monotypic genera, *Amynothrips* and *Vogtia*, that are simply stenophagous. The remaining five species are of *Agasicles*, which is entirely oriented to the amphibious amaranths (stenophagous). Unlike *Agasicles*, both *Amynothrips* and *Vogtia* have undergone evolutionary change without speciation. Low variability or intensive gene flow or both, to which Haffer (1974) attributes monotypy in numerous genera of South American birds, may account for the monotypic character of *Amynothrips* and *Vogtia*. Also, the different levels of speciation among these unrelated specialized insects may represent different stages of the taxon cycle, as postulated by Ricklefs and Cox (1973) (see p. 28). As compared with *Agasicles*, we note that *Disonycha argentinensis* has not split up into taxonomically distinguishable forms. Also, it is replaced by fasciate *Phenrica* species over much of the Amazon Basin (fig. 35). The replacement of vittate disonychine flea beetles by fasciate forms occurs with respect to several wide-ranging South American host plants (Vogt and Cordo 1976).

In table 2, the penetration of the alligatorweed geographic range by the 11 most specialized species shows a wide range of variation. If the species of *Agasicles* are excluded, the smallest (19.2 percent) and the largest (82.4 percent) penetrations are registered by the two very divergent (not phyletic) *Melanagromyza* species, one of which, *M. alternantherae*, is a leaf miner and the other a gall former. The very large range of the leaf miner completely surrounds the restricted range of the gall former. Because the speciation that has occurred in *Agasicles* is completely oriented to the amphibious amaranths and has resulted in almost complete geographic exclusion between the forms, the pene-

tration of the alligatorweed geographic range by the genus, 74.1 percent, is comparable with the penetration, 81.6 percent, achieved by the monotypic genus *Amynothrips* and 81.4 percent achieved by monotypic *Vogtia*. These three stenophagous genera may then be compared with the four species of the polyphagous genera as follows: *Disonycha argentinensis* with 41.4 percent penetration and each of the three agromyzid species with 82.4, 19.2, and 23.1 percent penetration. (*Disonycha argentinensis* is replaced by fasciate species of *Phenrica* over much of the Amazon Basin.)

Most of the 60 to 63 insect species of amphibious amaranths are concentrated in the region of the lower Paraguay River, the lower Paraná River, and two great estuaries, the Río de la Plata and the Guaíba River (region A, fig. 34). In this temperate to subtropical region we found 49 to 52 species affecting alligatorweed and *Alternanthera hassleriana*. Nineteen to twenty species were found feeding on alligatorweed and *Alternanthera sessilis* in the warmer northeastern extension of this region along the craggy east coast of Brazil, the Atlantic forest region of Müller (1973) (regions B and C, fig. 34). To the north, in the region inhabited by the Paraguay River form of *Agasicles opaca* and including the vast wetlands of the Pantanal of the upper Paraguay River (region D, fig. 34), we found 21 to 22 species affecting *Alternanthera hassleriana* and alligatorweed.

We found only 16 to 17 species of insects affecting amphibious amaranths in the vast Amazon Basin. Whereas the specialized species were well represented, the generalized to less specialized species were not, owing partly to sampling error. However, in the Lower Basin and Middle Basin, we feel that the lack of insects is more due to scarcity of amphibious amaranths, poor development of herbaceous flora as a source of alternative host plants, and greater habitat instability resulting from the magnitude of the hydrographic flux, which annually may attain 20 meters between maximum and minimum levels at Manaus (Sioli 1975).

In the Lower Basin and eastern Middle Basin (northern portion of region E, fig. 34), we found only 7 to 10 species of insects, mostly on *Alternanthera hassleriana*, but also on *A. sessilis* and alligatorweed, which are rare plants. In the upper reaches of the Madeira River, including the vast Plains (Llanos) of Mojós (southern half of region E, fig. 34), where the hydrographic flux is much less and *Alternanthera hassleriana* is widespread, we found only five species of insects affecting this

plant, near Trinidad, Bolivia. Alligatorweed was rare and limited to disturbed soil in the town. In the western Middle Basin and Upper Basin below the smaller tributaries (northeastern extension of region F, fig. 34), we found only nine species of insects on alligatorweed and *Alternanthera sessilis*, near Leticia, Colombia. In the Amazonian tributary valleys of the Andean foothills (southeastern portion of region F, fig. 34), we found only eight species on alligatorweed and *Alternanthera sessilis*.

Outside the areas where *Agasicles* is known to occur indigenously, we have the following results of insect surveys on amphibious amaranths. In South America, the Atlantic watershed north of the Amazon Basin yielded only nine species on alligatorweed, in the vicinity of Georgetown and on Trinidad, West Indies. The adjacent Caribbean watershed to the east yielded only six to seven species on *Alternanthera sessilis* (Vogt et al., cited in footnote 8). The Pacific watershed west of the Andes and north of Lima yielded only four species on *Alternanthera sessilis* and the transitional amphibious amaranth *A. halimifolia* (Vogt and Cordo, cited in footnote 15). In North America, in Panama and Mexico, we found only 7 species on *Alternanthera sessilis* and *A. obovata*, while in the Southern United States, we found 35 species on alligatorweed. All these insects are generalized to less generalized species (Vogt et al., cited in footnote 8). The comparatively large number found in the Southern United States is due to more extensive surveys and also reflects the abundance and dominance of the host plant, which exceeds by far any incidence seen in South America.

The greatest concentration of insects affecting amphibious amaranths in the alluvial areas of southern South America is centered in the lower Paraná and Paraguay Rivers and associated regions and may be related to a greater overall indigenous incidence of the host plants in this vast region of wetlands (MacArthur and Wilson 1967; Janzen 1973). This region has extraordinarily diverse, extensive insolated aquatic and subaquatic habitats. We believe that this diversity may exceed that of the lower and middle Amazon River and be older geologically (Stose 1950; Russell 1967). The lower Paraná and Paraguay Rivers and associated wetlands are probably a more stable habitat (less hydrographic range and a richer herbal flora) and may have been the most important centers for the radiation of some insects that feed on amphibious amaranths, for example, several ceccidomyiids,

several specialized agromyzids, and the alligatorweed flea beetles, *Disonycha argentinensis*, *Agasicles hygrophila*, and *A. opaca* (Paraguay River form).

As shown in figure 32, we have found no records of alligatorweed occurring west of the eastern coastal region of northeastern Brazil except in two subcoastal montane oases, Serra de Baturité¹⁶ and Serra do Tombador (at Jacobina).¹⁷ Besides, as shown in figure 34, we have no records of *Agasicles* from anywhere in this region. Our experience at Fortaleza, Ceará State, and inland, but not as far as the base of Serra de Baturité, indicates that the region is too dry. But within the Amazonian belt of heavy rainfall, in the vicinity of Belém and farther northwestwardly along the coast at Georgetown, alligatorweed is common, but again we found no trace of *Agasicles* even though conditions seemed to be generally favorable. Furthermore, we have found alligatorweed only rarely and no trace at all of the vittate *Agasicles* species between Belém and Manaus. We conclude that there is a separation in the distribution of alligatorweed across northeastern Brazil and a much broader void in the occurrence of *Agasicles* especially between the vittate species.

Haffer (1969 and 1974, p. 20) indicates that forest, and presumably appreciable rainfall, formed a narrow connection west of northeastern Brazil, between the forests near the mouth of the Amazon River and those of southeastern Brazil in the not very distant past. Generally, Haffer (1974, pp. 145 and 151) and Müller (1973) show no presumed forest refugia in northeastern Brazil except along the eastern coast during arid periods of the Pleistocene (figs. 86 and 87). However, existing mesophytic vegetation on Serra de Baturité and Serra do Tombador suggest that they may have served as refugia in times more arid than the present.

There is mounting evidence that in tropical South America climatic fluctuation during the Pleistocene and early Holocene caused rain forest to alternately contract and expand around more than a dozen widely distributed refugia of relatively small area. Dry savannah separated these refugia during

¹⁶Herbarium of Jardim Botânico de Rio de Janeiro, No. 44427: "Baturité, a margem os Rio Cambea 'Condea de cima' Serra de Baturité; José Eugenio (S.J.) #539 19-VIII-37 det. Joacim T. A. Fakis."

¹⁷On 19 Feb. 1962, Prof. Alexandre Leal Costa, Universidade de Bahia, presented us with specimens of alligatorweed he had collected 330 kilometers inland from Salvador, at Jacobina, Bahia, 610 meters elevation.

periods of minimal rainfall. Many of the rain forests rejoined during periods of maximal rainfall. These oscillations caused vegetational change and faunistic extinctions but also provided the isolation necessary for numerous animal populations to speciate (Müller 1973; Haffer 1974). Much of the faunistic differentiation in lower categories (subspecific through generic) is considered to have taken place during the past 800,000 years (late Pleistocene and Holocene) (Haffer 1974).

Thus far, only refugia on terra firma have been considered. While Müller (1973) takes up both forested and unforested dispersal centers, he recognizes no comparable refugia in alluvial lands, which encompass most of the habitats of amphibious amaranths and the *Agasicles* species that infest them. Biotic diversity of South American alluvial lands remains largely unexplained. Alluvial lands must have been subjected to various hydrographic regimes during the climatic oscillations, and their lower and middle reaches must have been subjected to transgressions of the sea. In the case of the lower and middle Amazon River, a magnificent estuary 2,500 kilometers long existed a few thousand years ago. Since then, the present alluvial plain has been laid down as a rapidly advancing delta (Russell 1967).

The interglacial seas that apparently engulfed the lower Paraná River up to its confluence with the Paraguay (Vuilleumier 1971) could have only partly extirpated alluvial biota, because of the refugium afforded by the Paraguay River and the Pantanal. Similarly, during glacial advances, this refugium, as well as the exposed Continental Shelf to the northeast, must have enabled survival of most forms as the climate became colder. The narrow littoral of the Brazilian east coast is considered to be a result of late Tertiary and earlier faulting (de Oliveira 1956; Axelrod 1960).

Measurement of alluvial fill in the Mississippi Valley has reliably established the minimum sea level attained during the last major glaciation as 138 meters below the present still stand, and this was reached after a major fluctuation in the rise from the minimum level reached about 50,000 years ago. It is further considered "that no higher stand of Pleistocene sea level exceeded today's stand by more than 10 meters" (Russell 1967). This range of glacio-eustasy conceivably could have isolated populations along the narrow littoral of Brazil, which in places is walled on the inland side by sheer granitic escarpments. In places, these are lapped by the present sea level.

Fossil and other evidence demonstrates clearly that numerous plants, such as *Nipa* species, and various insects, such as *Glossina* species, have migrated far and may no longer occupy their region of origin (Good 1953; Smith 1962; Ross 1974; Raven and Axelrod 1975). It is conceivable that a plant species' most ancient stronghold can have lost much of its insect fauna because of shrinkage of the area of occupancy or unfavorable environmental (e.g., climatic) change or both. Such a relict area may be faunistically depauperate as compared with more recent and more favorable (usually larger and more diverse) areas of occupation.

Our findings in South America may be partly explained by the proposal of Janzen (1968, 1973) and Opler (1974) that a host plant and its phytophage in continental areas are subject to the theories of island biogeography (MacArthur and Wilson 1967); that is, the number of insect species supported by a plant species increases as the host increases in area of geographical occurrence, in ecological diversity of occurrence, and in biomass. However, Opler (1974) notes that "the application of island theory to the number of species found on host plants is in opposition to the geologic time theory which holds that the number of insect species now found on host plants is a function of the age and abundance of the hosts in geologic time." Additionally, he notes a third theory "that offers an explanation for the varying numbers and densities of herbivorous insects of different host plants. [It] is based upon varying levels of chemical and physical defenses which have been evolved by plants [to escape insect attack]." A fourth theory (Slobodkin and Sanders 1969) relates environmental predictability to species diversity. Under this theory, highly predictable areas allow for greater species diversity. Such a relationship may be consistent with the greater faunistic diversity of alligatorweed in the basin of the Río de la Plata as compared with the lower Amazon Basin, which we consider to be a less stable environment for this amphibious amaranth.

Ecological and Evolutionary Considerations Within *Agasicles*

If the theories of island biogeography (MacArthur and Wilson 1967) apply to the host plant and its phytophages on continents, as postulated by Janzen (1968, 1973) and Opler (1974), it may be that the stage of speciation is important for judging the po-

tential of a biotic agent for weed control, because speciation, at least in its earlier stages, and subdivision of geographical range are usually one and the same process; and this process advances the taxon cycle. This cycle expresses the expansion and contraction of the geographical range and population density of a species or higher taxonomic category (Ricklefs 1973); and Ricklefs and Cox (1972) postulate for island birds, the "progress of a species through the taxon cycle reflects effects of progressively reduced competitive ability caused by 'counter-evolution' of an island biota to the species coupled with strong competitive pressure from subsequent immigrants." *Agasicles* may exemplify this possibility when its speciation is compared with the speciation of other important insect genera that attack alligatorweed. The monotypic genera that are almost coextensive with alligatorweed in South America, *Vogtia* and *Amynothrips* (table 2), may represent stage I of the taxon cycle described by Ricklefs and Cox (1972). In contrast, *Agasicles*, with a similar geographic distribution, is divided into five species that may represent stages II and III of the taxon cycle. (We will later show that one of these species is polytypic and that the others belong to a superspecies.) From this proposal, we may consider that *Agasicles* is the older "immigrant" to alligatorweed (the "island"), while *Vogtia* and *Amynothrips* are the more recent "immigrants." Therefore, speciation in *Agasicles* contrasted with the lack of it in *Vogtia* and *Amynothrips* may indicate a lower level of suppressive capability (lower suppressive index) for *Agasicles*. Moreover, the fasciate subspecific forms of *Agasicles opaca*, by virtue of being at an earlier stage in their speciation within the genus, may have a higher suppressive index against alligatorweed than their vittate congeners despite greater prevalence of their normal host, *Alternanthera hassleriana*, in South America. However, differences in dispersal ability among the specialized alligatorweed insects may be important because Ricklefs and Cox (1972) point out for some birds, especially the migrating species, that their dispersal power prevents movement of some forms through the taxon cycle.

Aside from the counterevolutionary effects that may be involved in its progress, the taxon cycle may, in the case of phytophage systems, be a taxonomically recognizable form of the evolutionary process that leads to host-parasite or host-predator homeostasis (Ricklefs 1973). This result of the counteradaptive or genetic feedback mechanism existing between interacting hosts and predators (or

parasites) has been applied in characterizing and in selecting biocontrol agents. Those that have had a long and close association with a host often do not severely suppress it because of high host-parasite homeostasis, there "having been a selection for resistance in the host and for non-virulence in the parasite" (Pimentel 1963, 1968; Harris 1973). On this basis, Pimentel (1963) urged biocontrol workers in their foreign explorations to seek agents infesting hosts related to the target species rather than the target species itself. Harris (1973) notes further that specialized oligophagous agents more than generalist polyphagous agents, as a rule, have high host-parasite homeostasis and may not be successful in biocontrol programs. Pianka (1974) states it this way: "Individual organisms with narrow tolerance limits, such as highly adapted specialists, generally suffer greater losses in fitness due to a unit of environmental deterioration than generalized organisms with more flexible requirements, all else being equal."

Evolution of host-parasite homeostasis is clearly a coevolutionary process, and later (p. 117), we will show that evolution of host-parasite homeostasis can be considered to be counterevolutionary. Laboratory studies show that the rare member of the interacting set of species is favored by evolution apparently because intraspecific competition is reduced, permitting evolution of greater efficiency in interspecific competition (Ricklefs 1973). Under the limitations of very finite conditions, laboratory experiments show clearly that the process is genetically determined, can transpire within the brief period of a year or two, and can result in little to imperceptible outward change in the physical form of the organisms involved (Pimentel et al. 1965). On the other hand, in its advanced stages, the taxon cycle results in morphological and ecological divergence that may attain differences on the species level. For these changes to occur, geological time is necessary, but the time needed is shorter on geographic islands as compared with the mainland. Also, as the taxon cycle progresses in island birds, the ecological niches of the interacting species are likely to change. When this occurs in phytophagous biocontrol agents, coevolutionary processes may be diluted by other evolutionary processes. Later, we will show that progress of *Agasicles* through the taxon cycle may be driven by coevolutionary rather than by counterevolutionary processes. Ricklefs and Cox (1972) note further that after the taxon attains stage IV of the cycle (endemic to one island and monotypic) increasing rarity

may either lead to extinction or provide significant release from counterevolutionary pressure. If the latter occurs, the species may again increase and begin a new cycle of invasion of the islands. A semblance of this process may exist in the subspecific forms of *Agasicles opaca*, to be considered later. The considerations above require a closer examination of the course of speciation in *Agasicles*.

All five species of *Agasicles* are remarkably alike in their adaptation to the aquatic and subaquatic habitats of the amphibious amaranths. These adaptations are both behavioral and structural and involve all the life stages. They are, in the best sense of the word, generic and very likely constitute the base from which radiation of the five forms took place. This differentiation appears to have taken place at least in its initial phases in geographical isolation (Mayr 1970; Diamond 1973) in two principal ways.

First, there was regional divergence in adaptation to climate, to geographic and ecotypic forms of the host plants, and to predators. Some of these adjustments are manifest in insect body size and form and in the form of markings, e.g., mimicry of their principal predator, a coccinellid beetle, by the three forms of *Agasicles opaca*, the fasciate species. Regional adaptations are also manifest in seasonal and habitat shifts within species as well as in actual habitat divergence among species. For example, within *Agasicles vittata*, the Peruvian population is subject to a less severe dry season than the Bolivian population. The forms of *A. opaca*, the fasciate species, are almost exclusively associated with *Alternanthera hassleriana* in insulated lagoons, whereas the vittate species are primarily associated with alligatorweed. *Agasicles vittata*, *A. interrogationis*, and *A. connexa*, which occur in subtropical to tropical climates are more active during seasons with increased cloud cover, as well as in the shade of the forest, whereas *Agasicles hygrophila*, a temperate to subtropical species, is more active in spring and fall but persists in summer if shade is available.

Second, regional speciation required the development of isolating mechanisms in zones of secondary contact between diverging populations, particularly in the zones of secondary contact (Mayr 1970; Haffer 1974). This evolution is manifest in the remarkably divergent external lock-and-key genitalia (figs. 2–6) and in less conspicuous changes in the uncleared aedeagi (figs. 27–31). Differentiation among species is remarkably attained in the vittate *Agasicles* species (figs. 2–5

and 27–30). However, we have not found appreciable differentiation in either the external genitalia or in the uncleared aedeagi within the wide-ranging and variable *Agasicles opaca* (figs. 6, 9, and 31). We conclude that this lack of differentiation in reproductive organs indicates a lack of reproductive isolation between populations. Later, we will consider this contrast between the vittate and fasciate *Agasicles* forms.

We note, too, that the lock, confined to the males, could serve as a generic character because it is a conspicuous and universal feature in the genus. But in females, the pygidial key is not sufficiently developed in two species (figs. 2 and 3) to be useful taxonomically. If it were unmistakably recognizable in the females of all species, the lock and key would qualify as a generic character. Presumably, the basic enlargement of terminal abdominal segments evolved in compensation as the flea beetle became more slender in conforming to the host-plant stem. It evolved simultaneously with the other generic characters. Then, the cavernous depression of the fifth male sternite and associated differentiation in both sexes probably evolved in the course of regional speciation.

The outline above assumes that an earlier wide-ranging species split up into geographical isolates and that the peripheral, more widely divergent forms probably broke off earlier than the proximal forms. This process “of slow genetic divergence and subsequent reproductive isolation of geographically separated and differentially adopted races or subspecies (Darwin’s ‘varieties’)” is the orthodox view among evolutionists (Dobzhansky 1972), and we illustrate it in figure 40A. Alternatively, the founder principle (Mayr 1970; Dobzhansky 1972) could apply. This process stems from the establishment of a new population by one or a few individuals in a region relatively isolated from the parent population. Initial inbreeding leads to a population with a changed gene pool that natural selection restructures under local conditions. Such a process could have occurred in the evolution of the forms of *Agasicles opaca* across the topography in the vicinity of the interface of the basins of the Paraguay and Amazon Rivers, as well as in the evolution of the vittate *Agasicles* species along the rugged littoral of eastern South America. If so, we believe the sequence of speciation would have been reversed from that resulting from the orthodox process outlined earlier; that is, the proximal forms appeared earlier than the distal forms. Compare figure 40B with figure 40A.

There is no evidence in any of the forms of *Agasicles* that specialization by resource partitioning has occurred. More specifically, there is no evidence of division of the habitat in the form of a common host plant. As a result, there is parapatry and allopatry within the genus. Because the *Agasicles* species are phylogenetically related, because the ecological niche of each species is so similar, and because each of the species has such high niche-exploitation potential, adjacent sets of species are ecological homologs (Vogt and Cordo 1976) and are subject to the competitive exclusion principle (Hardin 1960; Pianka 1974). Each of the four vittate species and each of the three fasciate forms of *Agasicles* are allopatric to parapatric. Only the more widely divergent vittate *A. hygrophila* and Paraguay River form of the fasciate *A. opaca* have overlapping ranges. Characteristically, all three fasciate forms occur on *Alternanthera hassleriana* in insolated lagoons. Only at a few sites about towns and other human disturbances between Asuncion and Resistencia does the Paraguay River form of *Agasicles opaca* occur on alligatorweed, and in these places *A. hygrophila* may also occur. We know of no other ecological difference between these two sympatric *Agasicles* species than the normal occurrence of the one on *Alternanthera hassleriana* in insolated lagoons and the other on alligatorweed.¹⁸ Of Schoener's (1974) five categories, this complementarity of niche dimensions seems to fit group 1: "Food type and habitat: The tendency for species that overlap in habitat to eat different foods." But the categorization is complicated by the fact that alligatorweed and *Alternanthera hassleriana* typically occur in different habitats. This fact may involve Schoener's (1974) developing theory of "feasibility of resource partitioning as it relates to particular dimensions." For our discussion two of his five considerations of dimensions are pertinent. They are: "Habitat dimensions are important more often than food-type dimensions, which are important more often than temporal dimensions" and "segregation by food type is more important for animals feeding on food that is large in relation to their own size than it is for animals feeding on relatively small food items."

Agasicles hygrophila and *A. opaca* occur side by side on alligatorweed near the lower Paraguay

River. Paul J. Spangler,¹⁹ in July 1969, found the first example of this sympatry in a pond in disturbed land near Asunción. Vogt and Cordo (cited in footnote 15) found another example in March 1976 along a ditch in the outskirts of the city of Formosa. The Paraguay River form of *A. opaca* also attacks alligatorweed along the shores of the diastrophic (nonalluvial) Ypacaraí Lake; the lake, 20 kilometers east of the Paraguay River, is completely free of *Alternanthera hassleriana*. In disturbed alluvial lagoons and ponds in the vicinity of Resistencia, Province of Chaco, *A. hygrophila* is also known to occur. Such occurrences are clear evidence that the two species are capable of competing at frequency-dependent levels (Ayala 1972) (see pp. 40 and 126). Under primeval conditions, such interspecific competition may have been either rare or a brief seasonal phenomenon. Important to these considerations of population interaction is the impressive long-distance dispersal capability demonstrated by *Agasicles hygrophila* in the Southern United States. In summer this cold-sensitive insect may reach inland more than 300 kilometers from permanent population foci near the Gulf of Mexico.²⁰ In comparison, the distance from Asunción to Necochea in southern Buenos Aires Province (the southern limit of the range of *A. hygrophila*) is about 1,500 kilometers, while the distance from Corumbá is 2,300 kilometers.

Should the range of *A. hygrophila* prove to reach the Pantanal of Mato Grosso, which is a distinct possibility, one might consider the Paraguay River form of *A. opaca* as representing character displacement between *A. hygrophila* and the *A. opaca* form of the Amazon Basin. We do not hold this view, however; we consider *Agasicles hygrophila* and *A. opaca* of the Amazon Basin as being too widely divergent in form, and we consider the Paraguay River form of *A. opaca* less widely divergent from *A. hygrophila* than either of the Amazonian forms. However, we view character displacement (Brown and Wilson 1956; Brown 1964) as a process by which closely related allopatric species may become completely sympatric in geological time within the dictates of the competitive exclusion principle (see p. 38). Also, an intensive 2-day search of the vicinity of Corumbá, Mato Grosso, in mid-April 1975 revealed only moderate numbers of the Paraguay River form

¹⁸On Ilha Careira in the lower Amazon, we also found 2 egg masses, presumably of *Agasicles opaca*, placed upon alligatorweed in a muddy pasture bordering a lagoon supporting *Alternanthera hassleriana* and *A. opaca* (Amazon River form).

¹⁹Personal communication, 10 Nov. 1970.

²⁰G. B. Vogt, P. C. Quimby, Jr., and S. H. Kay, "Progress of Biological Control of Alligatorweed in the Lower Mississippi Valley Region" (in preparation).

of *A. opaca* on *Alternanthera hassleriana*, with no trace of *Agasicles hygrophila* being found on the less prevalent alligatorweed.

Each of the five *Agasicles* species is quite clearly equally specialized for exploitation of its particular host plant in its particular geographic region and habitat. This probably stems from the similarity of the basic generic characters, described above (p. 30), of each species. The amount of geographic variation among the species indicates the degree of geographic divergence or derivation among the species. Thus, speciation in *Agasicles* has resulted primarily in geographic specialization rather than in change in host plant or in specialization on different plant parts. Adaptive changes within *Agasicles* as the taxon cycle progressed have been minor, except possibly the adaptation to the more specialized amphibious amaranth *Alternanthera hassleriana*. There is no evidence of any one form of *Agasicles* gaining a competitive edge over another form except in the case of overlapping *A. hygrophila* and the Paraguay River form of *A. opaca*. There is no evidence of *Agasicles* evolving into a new niche to avoid competition except possibly the adaptation of the fasciate forms to the more specialized

Alternanthera hassleriana, coupled to their evolution of mimicry of a principal predator, a coccinellid beetle which may be considered to be the model.

To close this section, we note that a refutation of the competitive exclusion principle may be considered to be in the results of the genetic feedback or counteradaptational experiments utilizing the competitive interaction of two muscoid flies, *Musca domestica* and *Phoenicia sericata*, under the very finite conditions of the laboratory (Pimentel et al. 1965). However, since *M. domestica* and *P. sericata* are distantly related, they are ecological analogs or nonanalogs (Vogt and Cordo 1975); and we hold to the view that the competitive exclusion principle will not have been refuted until comparable results are obtained utilizing a competitive interaction between two very closely related ecological homologs such as *Agasicles hygrophila* and *A. connexa*. Such results in the case of this example, at least, seem theoretically impossible because these two geographically exclusive species are probably optimally adapted to two slightly different climatic ranges. Even so, an intermediate simulated climatic regime might be adjusted to be equally suboptimal for each of the competitors and provide valid results.

PROPOSED EVOLUTIONARY DENDROGRAMS FOR FLEA BEETLES AND THEIR HOST PLANTS

Suggested Coevolutionary Course

The suggested evolutionary relationships of the flea beetle and plant species are presented in figures 39 and 40. The ancestral plant is generally terrestrial at point 1 and amphibious at 2 (fig. 39). The hollow compartmentalized stem must have existed when *Agasicles* and its ancestral forms appeared after having diverged from *Disonycha argentinensis* and its ancestral forms, presumably between points 1 and 2. We do not know the relationship of *Alternanthera sessilis* (subgenus *Alaganthera*) and of *A. obovata* to the evolutionary line leading to alligatorweed (subgenus *Telanthera*). As stated earlier, Pedersen (cited in footnote 6) considers *Alternanthera sessilis* to have affinities with Southeast Asian species. The Salvador, Bahia, form of alligatorweed is apparently a remarkable localized dimorphic form in which almost half of the population has stems bristling with erect hairs and most of the other half has glabrous stems. *A. hassleriana* is regarded by some botanists as an ecotypic (more hydrophytic form) of alligatorweed. However, the two forms occur side by side in disturbed sites. At point 3, inflated internodes are well developed.

It may be that the alternative host plants of *Disonycha argentinensis* are more recent orientations. But if alternative host plants corresponding to *Alternanthera kurzii*, *A. paronychioides*, and *A. pungens* existed at point A (fig. 40), colonies of the ancestral alligatorweed may have been necessarily isolated from their congeners in order for the evolutionary course to proceed. We assume such isolation as was needed existed at point A for both the ancestral terrestrial alligatorweed and its flea beetle. At that point, larvae had prominent setiferous tubercles, pupation was in the soil, and adults had a broad, short prothorax. But at point B, the host plant is beginning to develop amphibious tendencies, and the flea beetle begins to develop

adaptations to cope with the aquatic environment, possibly including prepupal stem entry. However, those entering oversized or undersized stems fail to survive.

Initial stem entry must have been by way of existing holes and open ends of severed stems and then by holes made large enough to enable passage of the fleshy tubercles and erect spatulate setae of the ancestral *Disonycha*-like larva. The large holes probably were plugged, judging by the behavior of existing soil-pupating species of *Disonycha* (p. 12). As natural selection reduced the size of the tubercles and setae, the making of smaller entrance holes evolved, causing less lodging of smaller stems and less flea beetle mortality. The making of the entrance hole must have involved extensions of larval responses into the prepupal stage. These include the positive chemotropic response to the host plant with the biting response, but without the response to ingest beyond the foregut.

For all seven *Agasicles* forms, there is no evidence of divergence in tropic responses to plants. All forms apparently are host-plant interchangeable within the amphibious amaranths. However, the *Agasicles* forms sort out geographically and by habitat in accordance with their adaptations. As a result, no species is known to attack, in nature, more than one or two species of amphibious amaranths. Our records show that, in the field, the Paraguay River form of *Agasicles opaca* and *A. hygrophila* develop in both *Alternanthera hassleriana* and alligatorweed and that *Agasicles vittata*, *A. interrogationis*, and *A. connexa* develop on both *Alternanthera sessilis* and alligatorweed. Also, no-choice testing shows that *Agasicles hygrophila* adults feed only sparingly on cut stem ends of *Alternanthera paronychioides* and *A. pungens*, with no perceptible development (Vogt and Cordo, cited in footnote 15). From these findings, it seems that *Agasicles*, in adapting to an aquatic environment, has been forced by natural selection to relinquish any terrestrial host-plant species it might

have had even when such plants are closely related to amphibious amaranths. As already noted, amphibious amaranths are plants of heterogeneous relationship, since *Alternanthera sessilis* and *A. rein- eckii* are members of a subgenus apart from al- ligatorweed and *A. hassleriana*, which are truly closely related.

D. M. Maddox²¹ has suggested that a special hy- groreceptor system may have evolved in *Agasicles*.

²¹Personal communication, 20 Apr. 1973.

Supporting this proposal is the more general host- plant range within *Alternanthera* exhibited by *Disonycha argentinensis* as compared with the lim- ited range of amphibious *Alternanthera* open to *Agasicles*. However, we are intrigued by the fact that *Agasicles* species are attracted to host plants in water, whereas *Alternanthera*-oriented *Disonycha* species normally avoid plants in water. Both re- sponses are remarkably clear-cut in the field. This contrast causes us to consider the possible evolution of opposite responses for a homologous receptor. In the evolutionary course there could have been

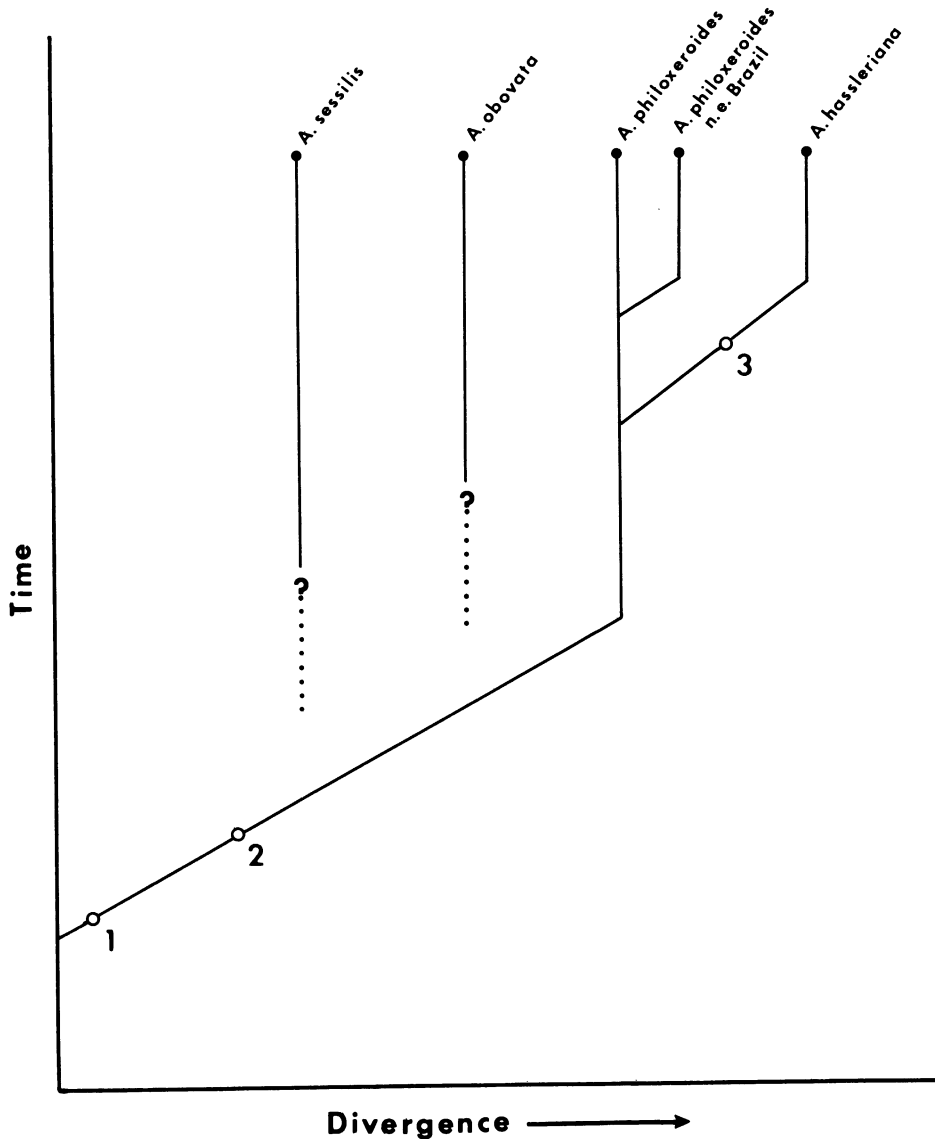


FIGURE 39.—Dendrogram of estimated evolutionary courses of four species of amphibious amaranths from a presumably terrestrial ancestral form.

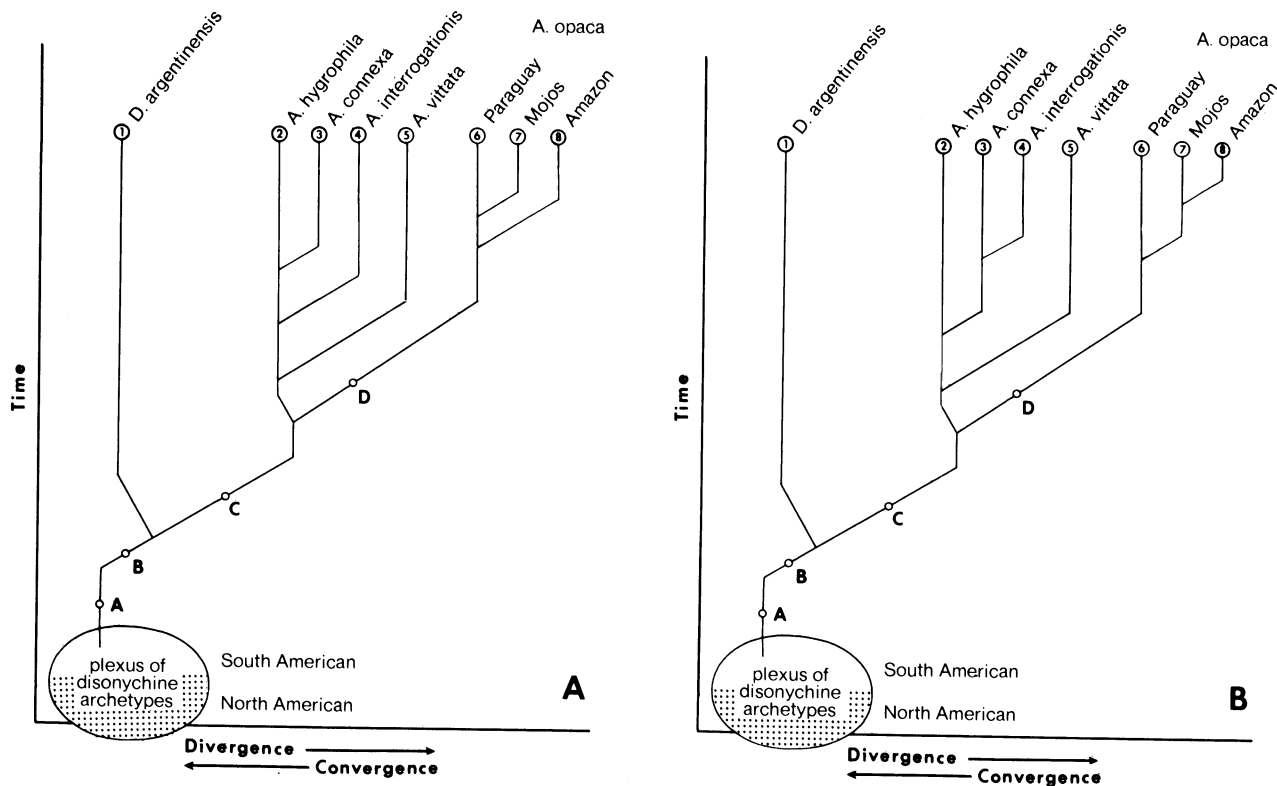


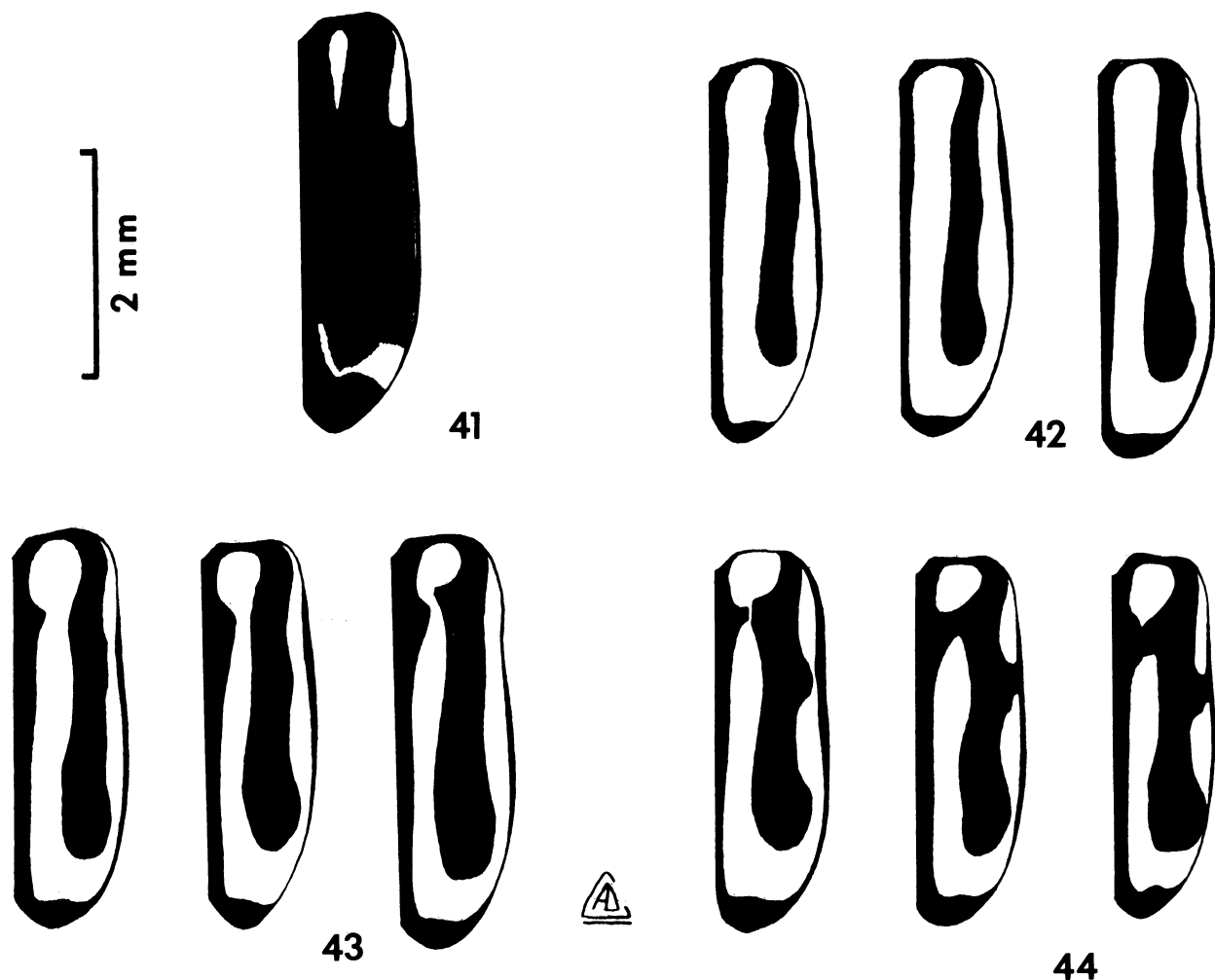
FIGURE 40.—Alternative dendrograms of estimated evolutionary course of *Disonychia argentinensis* and five *Agasicles* species from an ancestral form resembling *D. argentinensis*. Three geographic forms of *A. opaca* are indicated. A, Assuming the splitup of an earlier, wide-ranging species. B, Assuming speciation occurred by the founder principle (see p. 29).

a continuum of response intensity either way. A special hygroreceptor system may not necessarily be involved.

Not far beyond point B (fig. 40) the ancestral form of *Disonychia argentinensis* diverges from that of *Agasicles* and then undergoes some convergence entailing readaptation toward a more terrestrial habitat, while the ancestral form of *Agasicles* continues to adapt to the aquatic portion of the host plant's ecological range. If alternative host plants existed, the divergence would have occurred at an earlier point in the lineage in order not to require the convergent phase in the evolution of the ancestral form of *Disonychia argentinensis*. Under this condition, the convergent phase might be tantamount to divergence between that lineage and the one attached to alternative host plants and ancestral alligatorweed away from the zone of isolation. This complication is not indicated by existing species. Also, as compared with *Agasicles*, *Disonychia argentinensis* has not split up into taxonomically distinguishable forms (see p. 25). This contrast seems to be related to the interaction between the host stem and flea beetle.

At point C, prepupal stem entry is obligatory, T-shaped posterior processes are fully evolved in the pupae, reduction of larval setiferous tubercles is nearly complete, and development of hydrofuge pubescence and narrowing of the prothorax and elytra in adults are complete. With adaptation to the aquatic environment highly developed, radiation of the allopatric forms occurs in close succession. At point D, as the host plant develops the inflated internode, the ancestral form of *Agasicles opaca* develops a large, broad, more convex form and orange fasciate markings. The three forms of the Paraguay and the Amazon Basins diverge.

All the vittate species of *Agasicles* show a tendency for reduction and interruption of the U-shaped ivory-colored markings. This tendency is most pronounced in *A. hygrophila* and least pronounced in *A. vittata*. Figures 42–44 show representative variation in the markings of *A. hygrophila*. There is no evidence in these and many others of any lateral extension of the interrupted markings to form fasciae, such as occurs in the fasciate species of *Agasicles*. The greater tendency of *A. hygrophila* to have interrupted markings indi-



FIGURES 41-44.—Variation in elytral markings of *Agasicles hygrophila*. Figure 41 is an aberrant variant (Montevideo, Uruguay). Each group of 3 variants represents a percentage of the sample of 87 females and males as follows: 40 percent (fig. 42), 50 percent (fig. 43), and 10 percent (fig. 44).

cates affinity with the forms of fasciate *A. opaca* (compare figs. 41-44 with fig. 61).

Thus is estimated a course of interactive evolution of a distinct genus of aquatic flea beetles and a group of closely related amphibious host plants. The ancestral forms of both the host plants and of their dependent flea beetles probably were terrestrial. Alternatively, or at least in part, the evolution of *Agasicles* and *Disonycha argentinensis* could have occurred after the host plants had completed most of their evolution. This alternative would be more in accordance with the view that much plant evolution may have been accomplished before ancestral forms of recent insects became attached to them (Jermy 1976). According to Axelrod (1960), the fossil record shows that older Tertiary plants can be placed in existing genera and may even be similar

to existing species. However, the more fragmentary fossil record of phytophagous Coleoptera indicates some comparability in evolutionary progress. From North American Miocene deposits, Wickham (1920) and Hurd et al. (1962) list the modern chrysomelid genera *Trirhabda*, *Pyrrhalta* (*Galerucella*), *Diabrotica*, *Luperodes*, *Altica*, and *Systema*. Almost certainly *Disonycha* existed at that time. None of the 11 species listed is recent (Wickham 1920).

It may be that *Disonycha* has an older history in North America than in South America because there are species in North America, such as *Disonycha collata*, *D. xanthomelas*, and *D. triangularis*, that have relatively generalized host ranges and may therefore be more primitive. Also, a North American aquatic disonychine counterpart

to *Agasicles* may be *Disonycha pennsylvanica* and closely related forms. This group of species is characterized by costate elytra and is restricted to the Polygonaceae in subaquatic to aquatic habitats (Wilcox 1954; Blake 1955; Balsbaugh and Hays 1972; Vogt et al., cited in footnotes 12 and 15). The group ranges from Canada to Argentina, but it may be less obligatorily aquatic in South America. Besides *Disonycha pennsylvanica*, Blake (1933, 1955) lists five closely related species from North America and four other species from South America, including *D. bicarinata*, which we have observed at several widespread sites in Argentina. Unlike terrestrial *Disonycha*, this group of species has fine hydrofuge pubescence on its ventral surfaces. However, pupation normally takes place in wet duff and detritus near the margins of inundated areas. As prepupae, *D. pennsylvanica* will also enter existing openings in hollow stems of its host plant, as already cited. Although the *D. pennsylvanica* group is composed of somewhat more slender species than most other disonychines, the prothorax has not been narrowed and modified as in *Agasicles* (Vogt et al., cited in footnote 12). We believe that the aquatic disonychines of the Polygonaceae may be as old or older than *Agasicles*. They probably would be as strikingly distinct as *Agasicles* had they come into interaction with their host-plant stem. Even though they are adapted to the aquatic habitat, we do not consider the *Disonycha* with costate elytra as close extrageneric relatives of *Agasicles*, as much because of their consistent feeding relationship with the Polygonaceae as because of their structural divergences.

For comparison with *Agasicles*, there is another possible example of interactive evolution of a group of flea beetles that may have occurred as its host plants became aquatic from terrestrial ancestral forms. The divergence between the plants has been sufficient for water primroses, *Ludwigia* species, to be clearly distinct from terrestrial genera such as *Oenothera* and *Gaura*. From the inclusive genus *Altica*, Bechyné (1959) separated a group of very closely related aquatic flea beetles under the genus *Lysathia*. *Lysathia ludoviciana* of North America and *L. flavipes* and related species of South America, like the species of *Agasicles*, are specialized allopatric to parapatric vicarious species that are ecological homologs of one another. For its development, each is limited to aquatic and amphibious water primroses, especially *Ludwigia peploides*. In contrast, the terrestrial species, such as *Altica marevagans* and *A. foliacea*, are limited in

their development to terrestrial onagraceous hosts such as *Oenothera* and *Gaura*. *Altica litigata* of North America and various *Altica* species of South America are transitional in adaptation, developing on both amphibious and aquatic species of *Ludwigia*. Moreover, *Altica litigata* commonly develops on terrestrial *Oenothera biennis* (Vogt et al., cited in footnote 12).

The aquatic *Lysathia* resort to surface pupation when mud or some other soft, pliable substrate is not available for entry. The stems of *Ludwigia*, with their alternate leaf arrangement and lack of compartmentalized hollow stems, may not lend themselves to prepupal stem entry, thus accounting for the comparatively limited divergence between the aquatic *Lysathia* and the terrestrial to amphibious *Altica* species. There have been divergences, however, such as development of more highly specialized hydrofuge pubescence in the adult and more robust and adhering posterior processes in the pupa of aquatic species. But there has been no lateral restriction of body imposed by a host-plant stem and, consequently, no compensating increase in body length, with concomitant development of an enlarged and sexually dimorphic pygidium, a narrowed but elongated prothorax, and other structural changes that seem to have occurred in *Agasicles* in interactive evolution with the stem diameter of the host plant.

Alternatives to Coevolution

Hering (1951) describes the occurrence of disjunctions in host-plant spectra of certain leaf-mining insects that occur when a more or less distantly related plant becomes either acceptable or seasonally or geographically available as a new host. In view of this phenomenon there is need to consider further the recent transfer of indigenous North American terrestrial *Disonycha collata* and *D. xanthomelas* to alligatorweed. These somewhat generalized flea beetles may now have an opportunity to evolve an aquatic form comparable to *Agasicles*, just as the suggested ancestral form near *D. argentinensis* did in the geological past. Both North American flea beetles have adapted as effective suppressants of terrestrial alligatorweed. During flooding, adults of *D. collata* occasionally take refuge on floating mats of alligatorweed. We have found the mimetic predator-parasite of *Disonycha*, *Lebia viridipennis*, accompanying the temporarily displaced flea beetles. Such observations have been

made in the more northern, temperate latitudes, where the introduced *Agasicles hygrophila* may not become an important suppressant (Vogt et al., cited in footnote 12).

The transfer of two North American flea beetles to an introduced South American host plant constitutes a disjunction in host-plant spectra for two moderately generalized species. Earlier, these same flea beetles added introduced chenopodiaceous beet, spinach, and *Chenopodium album* to their host-plant spectra, when formerly they were restricted to North American species of Amaranthaceae and possibly *Stellaria* species (Caryophyllaceae). In these cases, the plant was brought by man into the indigenous range of the flea beetles and was accepted as a host. The proposed evolutionary history of *Agasicles* and the biogeography of the amaranth-feeding disonychine flea beetles point clearly to the probability of these disjunct host-plant transfers.

Disjunction in host-plant range may also evolve in situ between plant and transferring insect. In such cases, the transferring insect may undergo genetic changes in responses and tolerances and in habitat and nutritional requirements. A more or less distantly related plant may become an acceptable host as a result of coincidental or convergent evolution of phytochemical and other characteristics that attract, tolerate, and provide an adequate diet and habitat for a transferring more or less specialized, phytophagous insect. One of us²² has extensive evidence of this type of disjunction in Neotropical and Nearctic leaf-mining Buprestidae. In some species the transfer is limited to occasional eggs being placed on the disjunct host. In other related species all eggs are placed on the disjunct host, while the adults feed only on the ancestral hosts. In still other related species the transfer is complete, with all stages of the insect confined to the disjunct host. Transfer of insect species to new plants that are closely related to the ancestral hosts may also occur in the same manner. But such cases are inconspicuous and require close study for resolution. Analysis remains to be done of tens of thousands of rearings and field observations that may reveal clear evidence of this process in less disjunct, closely related host plants.

The various processes that lead to the formation of a disjunction in host range, whether they be coevolutionary or not, are extraneous (extrinsic) to

the coevolutionary process that follows orientation of an insect species to a new host. For definitive studies, we necessarily restrict our definition of coevolution to ongoing (intrinsic) interactions. Whenever they can be recognized, we either exclude or identify the extraneous phases. Ehrlich and Raven (1964), however, do not make this distinction in their concept of coevolution. Under this term, they include, with no exceptions indicated, "the stepwise [the steps may be diverse in size] responses on the part of the insect to the evolution of secondary plant substances" and other phytochemical attributes and structural and mechanical characteristics. They include under coevolution the new adaptive zones (mostly in the form of new host plants) that the stepwise responses open up to the insect under consideration. Also included is the reverse process in which the host plant resists or excludes insects by evolving a new phytochemical or physical protective system. Because the reverse process occurs during an ongoing biotic interaction, we also consider it as being intrinsically coevolutionary.

In host-plant disjunctions (stepwise shifts), although the phytochemical and other changes may have occurred passively or coincidentally with respect to the subject insect, these same changes in its new host plant could likely have resulted from the plant's interaction with other biotic agents having an extended prior history of association with that plant. This complexity is touched on by Ehrlich and Raven (1964) and may be the reason for their disregard for the extraneous phases that lead to particular coevolutionary processes. They stress the importance of considering the coevolution of insects and plants in the perspective of geological time, emphasizing that there must have been a succession of many and various interactants shifting from one evolutionary line of plants to another. From this it can be seen that for a given evolutionary line of plants, the interaction with a given evolutionary line of insects may be relatively brief. However, that same line of insects may continue on alternate host plants.

While many wide disjunctions seem to be clearly coincidental, narrow disjunctions in host-plant spectra probably more often involve essentially coevolutionary processes. The close ecological and genetic relationships within the plants and within the insects may result in such a complex of interactions that recognition of coincidental disjunctions would be impossible. Also, within these interacting guilds of species, oligophagous insects may lose

²²G. B. Vogt, unpublished studies.

one or more host species only to regain them later. Loss of a host-plant species may occur when plant resistance develops to the point of exclusion. Insect exclusion by host-plant resistance may be augmented more or less by the advantage gained through changing plant community characteristics, or plant defense guilds, as proposed by Atsatt and O'Dowd (1976). Such changes may deflect the chemotactic and other responses of the subject insect from the plants in question. The changes may also increase the pressure of the subject insect's predator-parasite complex. As stated earlier (p. 23), the feeding of *Disonycha glabrata* adults on alligatorweed, in addition to their feeding on normal hosts within *Chamissoa* and *Amaranthus* (including *Acnida*), may be either a transitional transference or a vestige of an old orientation to *Alternanthera*.

Also, reduction in stature or near extinction, or both, of a host-plant species may cause gaps in host-plant spectra. Extended geological time may be necessary for this process to take place and for appreciable gaps to appear. But in our time we are witnessing the demise of the American elm and the American chestnut as older trees. Simultaneously, numerous insects are losing important hosts, and some narrowly specialized dependent species are becoming extinct.²³

In applying the theories of island biogeography to the host plant and its phytophages on continents, Opler (1974) treats narrow to somewhat broader host-plant disjunctions in the following synthesis:

The relationship discovered between diversity of [lepidopterous] leaf miner guilds and the area of host [oak] occupation should be viewed in an evolutionary context. Through time, the number of leaf miner species feeding upon a given host will remain in equilibrium as the area of host occupation changes. The evolution of new species or extinction of previously existent ones maintains the equilibrium. By examining the taxonomic affinities and host relationships of extant leaf-miners in California, the source area from which new miner species are acquired by hosts of increasing distributional area can be readily envisioned. The source area for new colonists is only rarely some distant archipelago (another oak region), but is usually some sympatric host, although it need not be the closest related congener in the taxonomic sense. For example, three relatively unrelated oaks of northern montane affinities share the three closely related members of a single species complex of miners.

²³G. B. Vogt, unpublished notes.

In a similar vein, Janzen (1968) points out:

Island archipelagos are well known for the production of clusters of similar species from single founder species. The same thing appears to happen within insect groups, if the plant genus or family is regarded as the archipelago. By bridging the defensive system of a particular plant species, the insect species may now spread to other plant species with the same defense system [new adaptive zone] (e.g., Ehrlich and Raven, 1964).

Also, we note the degradation and detoxification of insecticidal canaverine in *Dioclea* seeds by a specialized bruchid as described by Rosenthal et al. (1977). Additionally, Rothschild (1973) cites numerous examples of disjunct host-plant patterns among aposematic insects that sequester toxins present in the food plant and thereby acquire protection against predators. Pharmacophagy orients such insects to "isolated genera of plants from unrelated plant families which share the same toxic secondary plant substances. . . ."

Stepwise coevolutionary patterns and the ability of the first organisms entering a new adaptive zone to increase its host spectrum and to radiate into species groups have prompted Ehrlich and Raven (1964) to reject a widely held idea, namely, the "theoretical picture of a generalized group of polyphagous insects from which specialized oligophagous forms were [are] gradually derived." As cogent, far sighted, and far reaching as their rejection is, it is conceivable that character displacement (Brown and Wilson 1956; Brown 1964; Mayr 1970), or ecological shift (Schoener 1974), may be a means by which the host-plant range of a species may be reduced or reduced at the same time that new hosts are added, disjunctly or not. For example, if *Disonycha glabrata* is considered to be the closest intrageneric relative of *D. argentinensis*, we may make the following speculations from the dendrogram shown in figure 45. Below periods A and B both Dg (*Disonycha glabrata* and its ancestral forms) and Da (*D. argentinensis* and its ancestral forms) were closely related allopatric species having the same host plants, *Alternanthera* species and *Chamissoa-Amaranthus* species. Within period A, the two species became partly sympatric and underwent character displacement with respect to host plant. In the area of overlap, Dg became partial to *Chamissoa-Amaranthus*, and Da became partial to *Alternanthera*. In period B, the overlap of the species expands to completion in

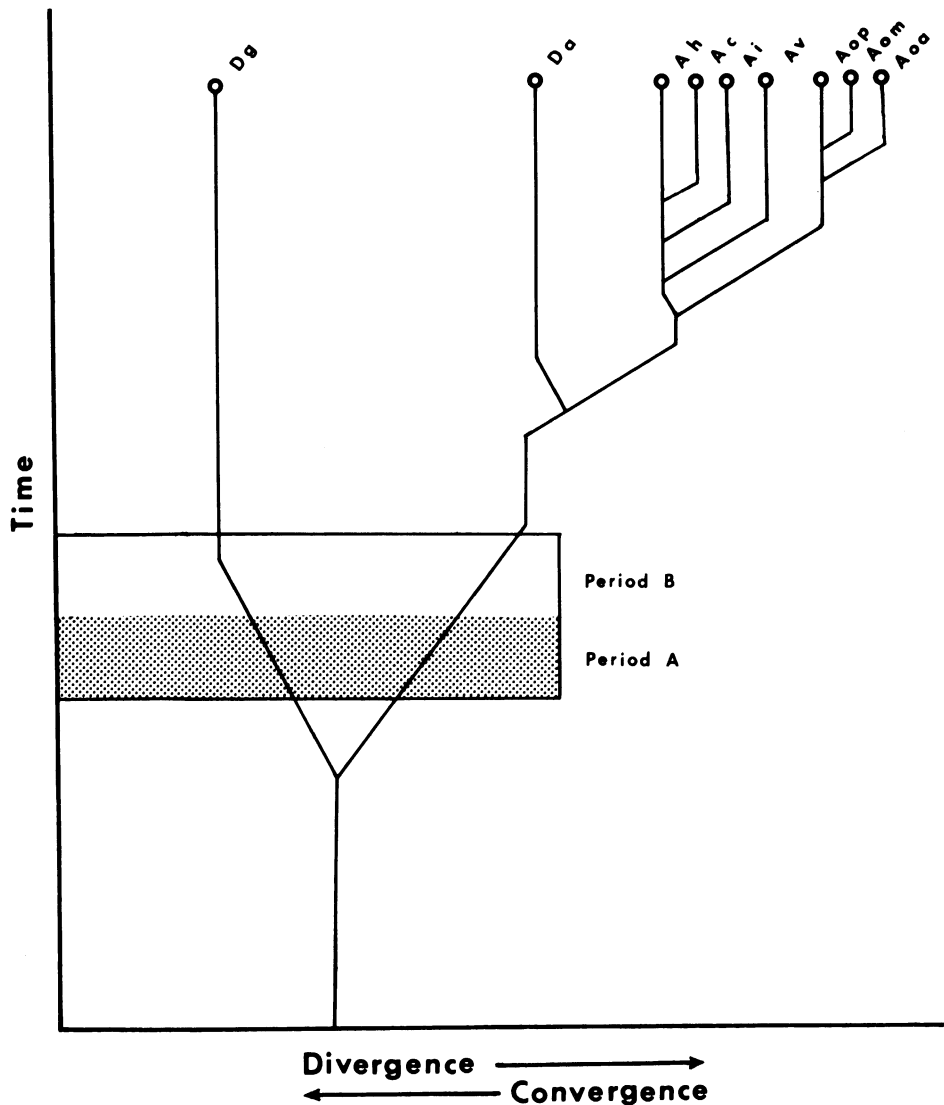


FIGURE 45.—Postulated evolutionary course of *Disonycha glabrata* and its ancestral forms (Dg) and *D. argentinensis* and its ancestral forms (Da), assuming that these two species are phylogenetically related. We have not studied the relationships between several vittate species of *Disonycha* similar in form to *D. glabrata*. We therefore assume subequal amounts of divergence and convergence with respect to division of host-plant spectrum. But this subequality does not likely apply to change of form. The difference in form between *D. glabrata* and *D. argentinensis* could most likely have resulted from divergence in the direction of *D. argentinensis*. Symbols Ah through Aoa represent the five species of *Agasicles* (species 2 through 8 on fig. 40).

South America, and all forms oriented to both *Chamissoa-Amaranthus* and *Alternanthera* are displaced. Above periods A and B, Dg and Da continue to be stenophagous, but on generically distinct host plants. They continue to diverge structurally, and Dg may have extended its range into North America by way of *Chamissoa* and *Amaranthus* (including *Acnida*).

There is evidence from studies of lizards and sun-

fishes that ecological shift can arise from phenotypic (behavioral) plasticity as well as from genetic changes (Schoener 1975; Werner and Hall 1977). As yet, we have not clearly identified shifts in host-plant spectra in insects because of phenotypic plasticity. However, testing under confinement often shows that insects have a somewhat broader host range than they are known to have in nature.

Because it applies to closely related species that

were originally allopatric, character displacement, or ecological shift, is important in the practice of biological control of weeds whenever one ecological homolog is considered for introduction to compete with another. It may be assumed that the homolog considered for introduction is the more aggressive species. If character displacement results in division of the host-plant spectrum shared between the two closely related species, in time either biotic agent or both may become increasingly suppressive because such a division in effect initiates an increase in host-plant specialization that may increase efficiency of host suppression (see p. 25). Conceivably, new host plants might be added during or after the division of the host-plant spectrum. Such extension of host-plant range might counteract the progress of host-plant specialization. Both the reduction and the extension processes would be aimed at attainment of geographical coexistence rather than at geographical displacement of one species by the other. Besides division of host spectrum, character displacement may occur in other ways that result in increased specialization: by division of the ecological range of the shared host-plant species; by division of the plant parts of the shared hosts; and by the development of distinct periodicity on the part of the insects. If character displacement does not occur, one of the homologs may either be displaced geographically or become extinct.

We note further that the taxon cycle would progress as speciation occurred by means of character displacement. At the same time, as Pianka (1974) points out, there would be a shift from r selection to K selection. These two opposing selective forces favor respectively the " r strategist" organism, characterized by high reproductive rates, and the " K strategist" organism, which subordinates reproductive rates to competitive or exploitative efficiency through specialization.

Conceivably, some previously allopatric, closely related phytophagous species may overlap in range and still coexist without ecological (including host-plant spectra) division or anatomical division of the shared host plants. We suspect that some of these species are likely ecological nonhomologs and nonanalogs (Vogt and Cordo 1976). Ayala (1972) has reported density-dependent coexistence in closely related saprophytic *Drosophila* species that may actually be cryptic (sibling) species. However, possibly applying in some species may be the character

convergence described by Cody (1973) in birds, mostly from the standpoint of flocking behavior. He believes that the consumer species involved may be either closely related (and possibly including ecological homologs) or distantly related (and possibly including ecological analogs). As compared with resource abundance when character displacement (character divergence) applies, the response of character convergence occurs when resources are in short supply and cannot support the consumer species separately. This would mean a single shared host plant or group of host plants instead of two or more separate host plants, each with a different consumer species. We believe that, in phytophagous insects, this process could either cause host-plant spectra to converge or prevent a host-plant spectrum from diverging. Ecological homologs and analogs as described by Vogt and Cordo (1976) may be involved in this process. But since weed problems do not, as a rule, involve resource scarcity, biocontrol workers may seldom become concerned with this process.

We have considered the process of coevolution as well as the coincidental and interactive processes that result in increases, decreases, and disjunctions in host-plant spectra. Before proceeding to the next section, we need only to briefly mention the importance of specialized insects in determining the composition of plant communities. We know that exotic plant species such as alligatorweed are aggressive invaders that often displace all other plants in certain habitats when introduced into regions lacking their specialized herbivores. Often, in their native habitats, such plants are of relatively low incidence, sometimes growing as members of mixed communities. This sparse occurrence is mostly a result of biotic suppression by specialized organisms, of which insects are a major component.

With this background and that given earlier on biology and biogeography of *Agasicles* and related flea beetles and their host plants and with the dendrograms in mind, we proceed to some quantitative studies of variation in the five species of *Agasicles* and the related *Disonycha argentinensis*. This presentation provides evidence for the evolutionary course of a genus of specialized insects interacting with the host-plant stem. We will discuss speciation, the possibilities of coevolution, and the finding of new, fully evolved host plants in the course of migrations.

MORPHOLOGICAL VARIATION IN FLEA BEETLES AND THEIR HOST PLANTS

The method described by Kim et al. (1963, 1966) provided the guidelines for much of the method for this study. Modifications are described below.

Measurement of Plants

The composition of the samples of host plants is given in table A-1 (appendix). Selection of plants to fit herbarium sheets was minimized by trimming large specimens to fit.

All specimens are from elevations near sea level to 95 meters, except those from the Huallaga River (610 m) and Pucallpa (160 m), Peru. The specimens were collected from February through May in 1960, 1961, and 1962, except for those from Leticia, Colombia, collected in June and July 1970. Except for eight specimens numbered 1,462,766 and 2,282,379 in the U.S. National Herbarium, all specimens are from 30 numbers in Vogt's herbarium within the series 1087 through 2138. All materials will be deposited in the U.S. National Herbarium.

The four plant dimensions used in the analysis are given in table 3. Measurements were also made of the stem diameter 80 millimeters from the terminal, the stem diameter at the middle of the fifth internode from the terminal, and the length of fifth internode from the terminal, but these dimensions varied too much to be useful analytical characters.

Vogt measured internode and stem lengths by stepping with a pair of dividers set at 10.0 millimeters. The remaining length, if any, was measured with a 10-centimeter portion of a Keuffel and Esser (KE) standard meter scale divided in 0.5-millimeter units. Stem diameters were measured directly with the KE scale; the measurements reported here reflect the shrinkage and internode collapse resulting from pressing and drying specimens. In living *Alternanthera hassleriana*, the maximum internode diameter is near the middle, but in the other aquatic amaranths, it is at the apex. Data on the reliability of measurements are given in table A-2.

Measurement of Flea Beetles

The composition of the flea beetle samples is given in tables A-3 and A-9 (appendix). All specimens are from elevations near sea level to 120 meters, except those from the Huallaga River, which are from 610 and 640 meters. The specimens were collected February through May in 1960, 1961, 1962, and 1975, except for those from Leticia, Colombia, collected in June and July 1970. All collections were by Vogt and his associates in the field, except for those taken by Paul J. Spangler at Luqué, Paraguay, and near Itabuna, Bahia, Brazil, in June 1969. All materials will be deposited in the U.S. National Museum of Natural History.

Collecting in all cases was done by observation rather than by sweep net. In those collections of which only a portion of the specimens was measured, individuals were picked at random from samples previously sorted into female and male groups, but overly teneral and damaged specimens were eliminated until the desired number of measurable specimens was attained.

We have not exhausted the possible dimensions for measurement of exposed body structures. Rather we selected those dimensions which seemed more likely to show a relationship with the host-plant stem diameter. We did not make measure-

Table 3.—Plant characters analyzed

Number	Character	Abbreviation
1	Stem diameter at midpoint of internode falling within 80 mm of terminal.	Int'n W1.
2	Length of that internode.	Int'n L.
3	Length of ascending stem (from last rooted node to terminal for lead stem).	Ascdng L.
4	Stem diameter at base of ascending stem.	Int'n W3.

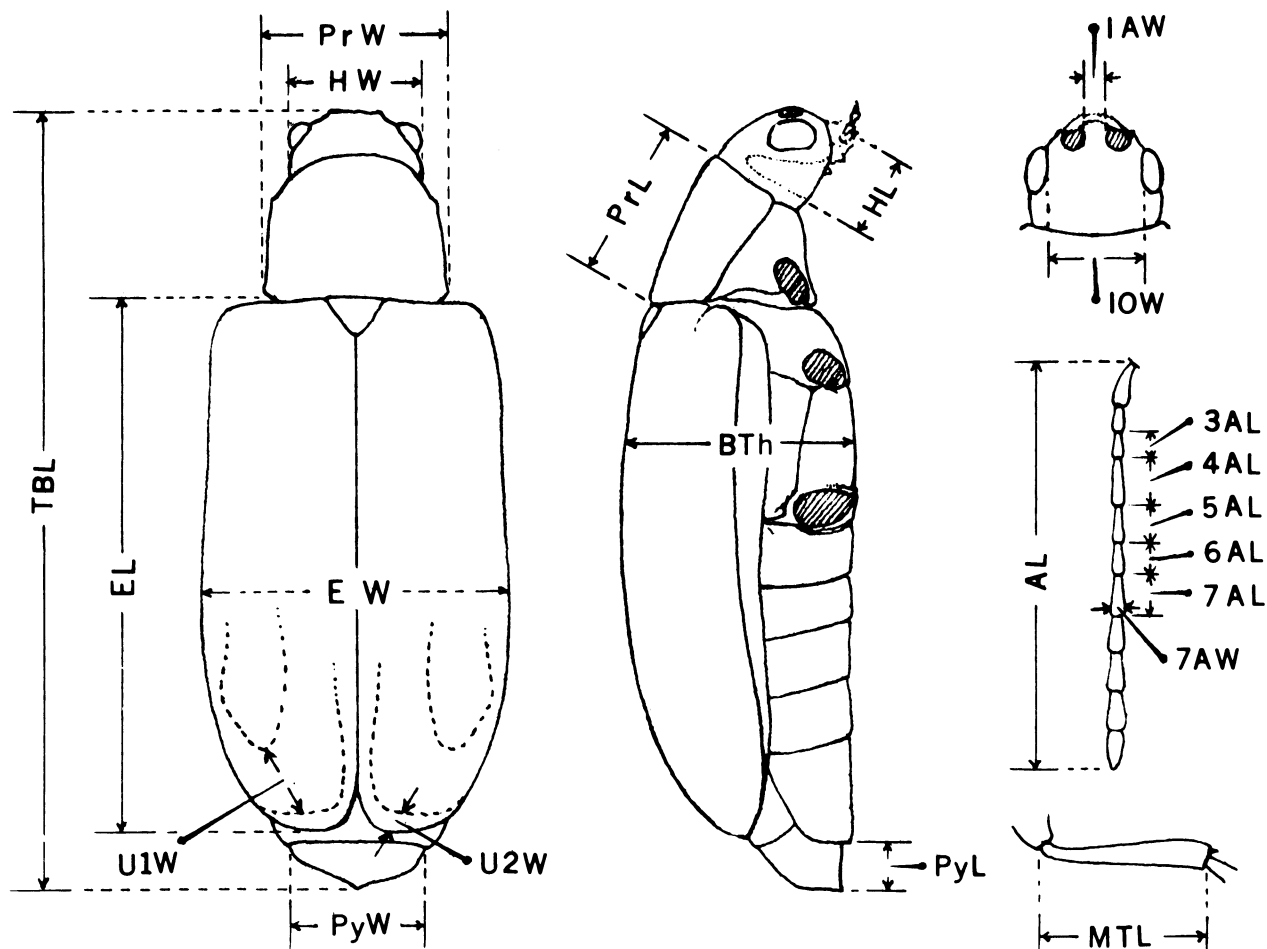


FIGURE 46.—Characters measured in flea beetles. The abbreviations are identified in table 4.

ments of the female spermathecae and the male aedeagi. Aside from the technical difficulties in their measurement, there is the problem of relating measurements of the female structures with those of the male. Such measurements, however, would have been more likely diagnostic from the taxonomic standpoint than have those we measured of the exposed body structures.

Of the 32 characters measured, 10 were not utilized in order to reduce the amount of work. They are length and width of the fifth sternite, apical width of pronotum, lengths of antennal segments 1, 2, and 8 through 11, and the width of segment 9. The 22 characters analyzed are illustrated in figure 46 and listed in table 4.

All measurements were made by Vogt, using a stereoscopic microscope equipped with 1×, 3×, and 6× objectives and 9× oculars, the left one being fitted with a linear graduated ocular micrometer 5 millimeters long, and the right one, with a reticule

having a 10-millimeter squared area (100 squares). Both of these micrometer reticules were calibrated with a stage micrometer to two significant figures for each of the three objectives. The linear micrometer was used for all measurements except for those appreciably exceeding the 5-millimeter linear scale at the given magnification but falling within the 10-millimeter squared area.

All specimens were preserved in 75 percent ethanol and were therefore in a relaxed condition. Each specimen was measured and read for all qualitative and meristic characters at one time.²⁴ This procedure was necessary to minimize the practical problems inherent in measuring and reading rather large-sized whole specimens that were oriented as needed on a wad of absorbent cotton and moistened

²⁴Most of the meristic and qualitative readings will be covered in a future paper.

Table 4.—Insect characters analyzed¹

Number	Character	Abbreviation	Objective	Aspect
1	Body length	TBL	1	Dorsal.
2	Body width	EW	3	Dorsal.
3	Body thickness	BTh	1	Lateral.
4	Head length	HL	3	Lateral.
5	Head width	HW	3	Dorsal.
6	Interantennal width	IAW	6	Dorsal.
7	Interocular width	IOW	6	Dorsal.
8	Pronotal length	PrL	3	Lateral.
9	Pronotal width	PrW	3	Dorsal.
10	Elytral length	EL	1	Dorsal.
11	Minimum internal width of elytral "U"	U1W	3	Dorsocaudal.
12	Maximum external width of elytral "U"	U2W	3	Dorsocaudal.
13	Pygidial length	PyL	3	Lateral.
14	Pygidial width	PyW	3	Caudal.
15	Length of metathoracic tibia	MTL	3	Anterior.
16	Antennal length	AL	1	Dorsal.
17	Length of 3d antennal segment	3AL	6	Dorsal.
18	Length of 4th antennal segment	4AL	6	Dorsal.
19	Length of 5th antennal segment	5AL	6	Dorsal.
20	Length of 6th antennal segment	6AL	6	Dorsal.
21	Length of 7th antennal segment	7AL	6	Dorsal.
22	Width of 7th antennal segment	7AW	6	Dorsal.

¹The characters measured are illustrated in fig. 46.

as needed with 75 percent ethanol in a syracuse watch glass. Each portion of the insect was carefully maintained on a horizontal plane while being measured.

Data on the reliability of the flea beetle measurements are given in table A-4. In connection with some of the high coefficients of variation, head length (HL) and pygidial length (PyL) each involve landmarks that have a contrast in focal plane with respect to the horizontal axis of the specimen oriented across the field of the microscope. In the case of the maximum external width of the elytral "U" (U2W) and the length of the third antennal segment (3AL), it is possible that the three measurements could have been made inconsistently on the right or left side of the specimen.

Two sets of measurements of flea beetles were made. The larger set was done during 1968-70 and is treated separately from the second, which was made during 1976-77 to incorporate additional sampling from the surveys made in 1975 in South America. In processing the 1977 data we discovered that Vogt had inadvertently applied incorrect calibration factors for the 3× and 6× objective measurements made during 1968-70. The incorrect calibration factors are 0.0312 and 0.00598, respectively, for the 3× and 6× objectives. The correct

values are: $C_{3\times} = 0.0344$ and $C_{6\times} = 0.0170$. We have not corrected the statistics presented in tables A-4 and A-6—A-8, nor have we corrected the scales of the graphs given in figures 50-60. However, we have adjusted the scales of the 1977 series of graphs (figs. 62-72) so that the phenoclines and normal ellipses are as nearly equalized in configuration and size with those of the earlier results as is practicable. We have not made the fine adjustments needed to fully equalize the configurations of the two sets of results because of the tedium and time required for this graphical method. However, the scale values given in the more recently prepared charts approximate the corrected values for the graphs of the earlier set. We feel some students will find it instructive, as we do, having the incorrect data presented. The pictorial aspect of the presentation is essentially unaffected. We note, though, that the mean points in figures 62-72 not central to the three plotted normal ellipses were calculated by non-machine methods, i.e., by slide rule. Although these calculations have been rechecked three times for accuracy, close comparison shows there are some minor discrepancies between them and the corresponding mean points of the earlier phenoclines that are based upon Wang 700 output (figs. 50-60).

All phenocline distances utilized in tables 5, 6, and

8 through 13 were measured with a 15-centimeter section of a Keuffel and Esser standard meter scale divided in 0.5-millimeter units. All measurements were made on the originals of the indicated graphs.

Correlation of Characters

Using a Wang 700 programmable electronic calculator, J. U. McGuire, Jr., developed and carried out a program to reduce the measurement data to common terms, obtain the mean and standard deviation for each of the plant and flea beetle characters, and obtain the corresponding coefficient of correlation and the points for each of the corresponding bivariate, normal, 95-percent-tolerance ellipses.²⁵ McGuire conceived the application of the normal ellipse.

In the graphs, each bivariate normal ellipse is centered on the mean point. For the flea beetle species, we postulate the same sequence for the mean points as we give for Recent time in the dendrogram that hypothetically represents the evolution of the six forms of flea beetles from a single ancestral form (fig. 40). Therefore, in each graph (figs. 50–60 and 62–72), we consider the line connecting the mean points of the species in this sequence as an evolutionary trend line for the particular pair of variables (characters) plotted on the graph. This trend line corresponds to the phenocline of Ross (1974).

After the correlation of characters in the plants, we will consider three different versions of the *Disonycha-Agasicles* phenocline. We will take up the first version (figs. 50–60) in the next section, "Flea Beetles (Recognized Species)" (p. 49). Next, we will consider the second version (figs. 62–72) in the section "Flea Beetles (Subspecific Forms of *Agasicles opaca*)" (p. 76). Last, under "Proposed Trifurcate Representation for the Phenoclines" (p. 103), we will consider the third version (figs. 74–84). In the third version, the order of the mean points is changed.

The bivariate normal ellipse encloses the area

containing 95 percent of the possible points (x, y) from a given population. The size and shape of each ellipse depends on the variances, correlations, and sample size from which the parameters were computed. If the variances are small, the ellipse is also small. If the two variances are equal and the correlation coefficient is near zero, the ellipse becomes a circle; as the correlation coefficient approaches 1, the ellipse degenerates into a straight line. If the sample size is small, the ellipse is large, decreasing with increasing sample size.

It should be stressed that the representation of our sample sets by normal ellipses is strictly a descriptive statistical technique. It is thus not intended that the graphs be used for purposes of statistical inference (i.e., testing hypotheses). In the judgments we have made, the graphs have been only one of many inputs.

The correlation coefficient is a parameter of the bivariate normal distribution. It is related to the angle that the major axis of the ellipse makes with the horizontal axis. If the angle is between zero and 90°, the ellipse is inclined to the right and the correlation is positive. If the angle is between 90° and 120°, the ellipse tips to the left, and the correlation coefficient is negative. Ellipses in parallel alignment indicate maximal intercharacter correlation, whereas ellipses oriented at various angles signify low intercharacter correlation. Characters having the least intercharacter correlation between the species tend to be more discriminant and therefore most useful taxonomically. Discrimination is expressed by the amount of separation or overlap among the ellipses representative of the species.

Plants

The means, standard deviations, and coefficients of correlation of the four plant-part measurements taken of *Alternanthera philoxeroides*, *A. hassleriana*, and *A. sessilis* are given in table A–5. The graphs (figs. 47 and 48) show the corresponding sets of normal ellipses for the three plant species. In addition, a few individual points are plotted for certain growth habits for which there was insufficient sampling.

In figure 47, stem size is expressed by length of the ascending portion of the stem and its basal width. It is strikingly clear that the ascending stem of floating decumbent *A. hassleriana* is remarkably short (ellipse B), and its ascending erect growth habit when competing with erect plants (points A) may equal or exceed the heights attained by al-

²⁵Late in this study McGuire reprogrammed on a Wang 2200 and corrected a slight error in the Wang 700 program, in which $k = 2F_{2, n-1} (n - 2/n - 1)$ was used instead of $k = 2F_{2, n-1} (n - 1/n - 2)$. We applied the Wang 2200 output in the following graphs (figures): 65A (Paraguay River form only), 65B (Plains of Mojos form only), and 66, A and B (all forms). In these figures, the indicated normal ellipses are a trifle larger than those based on the Wang 700 output (the value of k changes from about 7 to about 8).

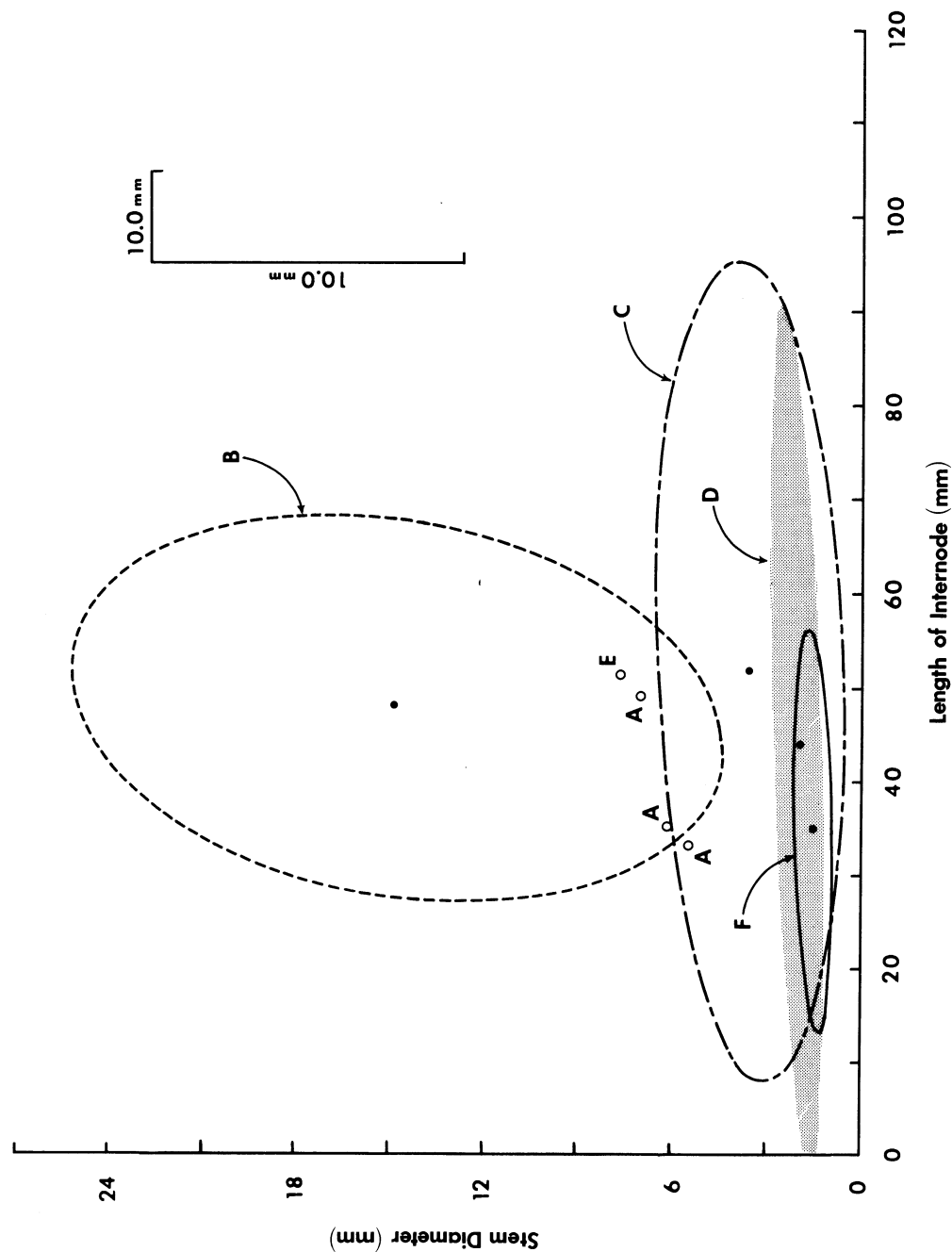


FIGURE 48.—Stem size in South American amphibious amaranths, by length and diameter at midpoint of stem internode reaching within 80 millimeters of terminal. A (three points), *Alternanthera hassleriana* ascending stem competing among large erect *Eichhornia* (near Asunción, Paraguay). B (normal ellipse and mean point), *A. hassleriana*, free floating but with cordlike attachment to lagoon bottom; the prevalent growth form. C (normal ellipse and mean point), *A. philoxeroides*, usually found competing among erect stems; all specimens collected within the range of vittate species of *Agasicles*; the prevalent growth form. D (normal ellipse and mean point), *A. philoxeroides*, regeneration of *Agasicles*-suppressed plants, Reconquista River near Buenos Aires. E (single point), *A. philoxeroides*, floating, possibly a form with cordlike attachment to lagoon bottom; collected south of the range of *A. hassleriana*, near city of Santa Fe, Argentina. F (normal ellipse and mean point), *A. sessilis*, usually found among competing erect stems; all specimens collected within the range of *Agasicles vittata*.

ligatorweed and *A. sessilis* (ellipses C and F). The stem diameter shows less clearly the greater stem diameter of *A. hassleriana* and the smaller diameter of *A. sessilis* than is shown in figure 48.

As observed by Chodat (1917), the floating stem of *Alternanthera hassleriana* is stabilized by a mass of fine roots extending beneath the water surface. They counterbalance the pair of erect leaves emerging above the water at each node, and a long ascending stem would interfere with this stability (fig. 7). Such stability and such a rigidly consistent orientation of leaves and of root masses are not evident in alligatorweed even when it is trailing on the ground. A floating growth habit that compares with that of *Alternanthera hassleriana* has yet to be found in alligatorweed.

Somewhat comparable with *A. hassleriana*, however, may be the stems emerging from the margins of incipient floating mats of alligatorweed that occur occasionally in South America or from the margins of the extensive, established floating mats that were commonplace in the Southern United States (see frontispiece). Each of these more or less isolated and noncompeting stems represents new growth; each emerges from the water surface in a broad gentle curve, ascending usually not more than 200 millimeters. A few such stems are included in the sample represented in figure 47 by ellipse C. But a single example from a lagoon near Santa Fe, Argentina, having exceptionally large-diameter internodes has been plotted separately on figure 47 (point E) for comparison. The grossness of this plant approaches that of the floating form of *A. hassleriana*, which is not known to occur so far south in South America.

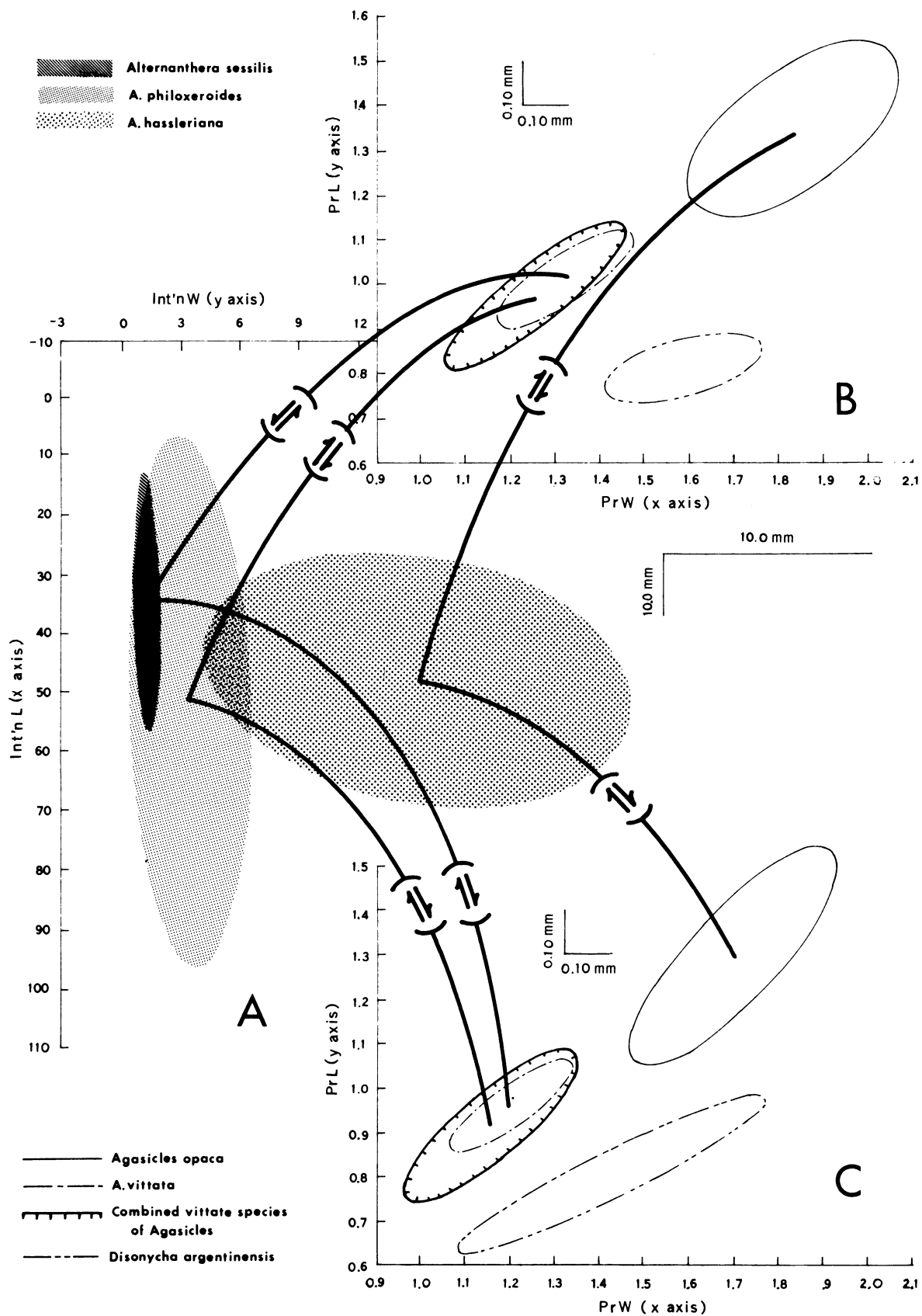
The lagoons near Santa Fe are in the broad flood plain of the Paraná River above its delta. They are insolated and resemble the lagoons in the Chaco, 500 kilometers upriver, where *Alternanthera hassleriana* grows to the exclusion of alligatorweed, at least in undisturbed lagoons. In the 500 kilometers separating Santa Fe and Resistencia, we do not know just where *A. hassleriana* reaches the southernmost limit of its range. We believe it is likely that this tropical plant does not reach appreciably beyond the confluence of the Paraguay River and the Paraná River. It is very unlikely that alligatorweed develops a floating, lagoon-inhabiting growth habit that really approaches *A. hassleriana* in form or intergrades with it.

The film of water covering its hydrophilic floating stems and the weight of its more robust ascending stems, together with their broad, heavy foliage,

may contribute to *A. hassleriana* having such short ascending stems when it is a more or less isolated, noncompeting, free-floating plant. In insolated lagoons in South America, *A. hassleriana* occurs either as isolated floating stems or as loosely woven mats in which ascending stems are of the usual very low profile. In contrast, the more or less free-floating, noncompeting stems of alligatorweed ascend with tapering, elongated stem internodes and slender leaves. These usually emerge from the margins of incipient (in South America) or established (pre-biocontrol in the Southern United States) floating mats of the plant. Dense floating mats with emergent, erect, competing stems 300 to 1,000 millimeters tall, such as alligatorweed formed commonly in the Southern United States, were never found involving either of these aquatic amaranths in South America.

Both plants have about the same ascending capability when competing with other stems. However, as indicated above, *Alternanthera hassleriana* does not ascend when competing intraspecifically in open lagoons. Almost all erect *A. hassleriana* plants observed in South America were competing in dense growths of *Eichhornia*. For either amaranth, the surrounding competing erect stems provide needed mechanical support. In addition, both in South America and in the Southern United States, alligatorweed stems have been found to ascend to heights of 2,000 to 3,000 millimeters by climbing from branch to branch of shrubs and bushes, which provide the needed mechanical support for these weakly rigid, normally trailing plants.

In figure 48, stem size is expressed by length and width at the midpoint of the stem internode reaching within 80 millimeters of the terminal meristem. Based upon the samples measured, which are representative of the prevalent growth habit of each plant species, the internode diameter and to a less extent the internode length of *A. sessilis* (ellipse F) are smaller. They fall almost entirely within the range of variations of alligatorweed (ellipse C). In contrast, the prevalent decumbent, floating growth habit of *A. hassleriana* (ellipse B) has only a narrow overlap with alligatorweed. It has a much larger range of internode diameter, but with internode length falling within the range of alligatorweed. However, more nearly like the growth habit of alligatorweed, but in marked contrast with its own floating, decumbent growth habit, are the ascending stems of *A. hassleriana* that compete with erect plants such as occur within rafts of giant *Eichhornia* (points A). These stems remain distin-



guishable from alligatorweed by their grossness, their vestigially inflated internodes, and often by their appressed surface vestiture.

Included in figure 48 is a representation of stem size of the alligatorweed regenerating uniformly in an area where the stems had been covered with silt along the banks of the Reconquista River near Buenos Aires (ellipse D). This alligatorweed had a history of heavy suppression by *Agasicles hygrophila*. These stems are almost as slender as stems of *Alternanthera sessilis* (ellipse F), and virtually every one was infested at the time of sampling by at least one clutch of first-instar *Agasicles hygrophila* larvae. Therefore, there was a high probability of attempted pupation within these stems at the same time that there was a low probability of appreciable growth in stem diameter during the 2 weeks needed for larval development.

The samples of alligatorweed were inadequate to show significant differences in diameter among stems from the four regions where each of the four vittate *Agasicles* species occur. This deficiency in sampling required combining all these materials for the comparative purposes treated in the next section. For similar reasons, the *Alternanthera hassleriana* materials from the Paraguay and Amazon Rivers were combined.

Field observations indicate wide variation in stem diameters of alligatorweed for any given locality but with no recognizable change geographically. *Alternanthera hassleriana* varies much less at a given locality and shows no appreciable difference between the basins of the Amazon and Paraguay Rivers.

Flea beetles (recognized species)

The means, standard deviations, and coefficients of correlation of the 11 pairs of flea beetle characters measured on the 6 recognized disonychine species are given in tables A-6 (females) and A-7 (males). Statistics are given in table A-8 and figure 49 (B and C) for the combined samples of pronotal width (PrW) and length (PrL) for all four vittate species of *Agasicles*.

Three of the bivariate normal ellipses in figure 48 (B, C, and F), which represent the prevalent

growth forms of each of the three species of aquatic amaranths, are shown again in figure 49A. Here they are shown in a suggested relationship with their disonychine flea beetles, which are represented by normal ellipses expressing the variation of the length to width of the pronotum for females (fig. 49B) and males (fig. 49C).

The flea beetles of the genus *Agasicles* are grouped geographically to correspond with the range and samples of the host plants (figs. 32-34). The Amazonian and Paraguayan forms of fasciate *A. opaca* are combined to correspond with the range of *Alternanthera hassleriana*. *Agasicles vittata* and its three other vittate congeners are combined in a unit to correspond with the range of alligatorweed. Inadequate sampling of the host plants prevented comparisons with individual species of *Agasicles*. However, *Agasicles vittata* is shown separately because, over part of its range, it is associated exclusively with *Alternanthera sessilis* (figs. 33 and 34). As explained earlier, this plant is also a host, but a minor one, for *Agasicles vittata* further downriver and for *A. interrogationis* and *A. connexa* along the narrow littoral of Brazil. In both of these regions, alligatorweed is the major host plant.

Because all these species of *Agasicles* pupate only inside their host-plant stem, each of the three sets of ellipses for *Agasicles* is connected by a line indicating interaction with the ellipse expressing variation of host-plant internode length and width. No interaction is shown between the ellipse for *Disonycha argentinensis* and any of the host plants because, as indicated earlier, this flea beetle pupates in soil.

More than any other measurements made in this study, pronotal length and width show clearly the reduction of flea beetle width caused by restriction of the host-plant stem diameter. A slender prothorax, together with a somewhat narrowed head, afford mobility within the stem internode cavity. This mobility is probably needed by the newly emerged flea beetle for feeding, either generally within the stem or in making an exit from the stem. Also, we point out that the length and width of pronotum in the pupa are nearly the same as in the adult (figs. 21-25). In contrast, this is not at all true of the elytra, to be discussed later.

In comparing the ellipses of graphs B and C of

FIGURE 49.—Interactive evolution of amphibious amaranths and *Agasicles* species that pupate in the stem. The interaction is most evident in the comparison of A, host-plant stem size (Int'n W and Int'n L), with B and C, pronotal size (PrW and PrL) for females and males of the infesting flea beetles. In *Disonycha argentinensis*, which pupates in soil, the pronotal width is much greater and the pronotal length much less than in the vittate species of *Agasicles*. (This figure is a composite of figs. 48 and 50.)

figure 49, representing the flea beetles, with those representing the host plants in graph A, it is evident that the stem diameters of *Alternanthera sessilis* tend to be undersized for the pupating flea beetles, while those of alligatorweed tend to be slightly oversized; those of *A. hassleriana* are markedly oversized. From this it may be concluded that *A. sessilis* has the most restrictive stem diameter and *A. hassleriana* the least (if at all) restrictive diameter. Also, both *A. sessilis* and alligatorweed, the normal hosts of the vittate *Agasicles* species, have more restrictive stem diameters than does, if it does at all, *Alternanthera hassleriana*, the normal host plant of the three fasciate forms of *Agasicles*. *Alternanthera sessilis*, however, does not occur within the range of the smallest vittate species, *Agasicles hygrophila*.

The ellipses for the combined vittate species of *Agasicles* show that reduced insect width was accompanied by a compensating increase in length. The fasciate forms, whose host plant has large stem cavities, has increased in overall size considerably beyond the dimensions of the vittate species of *Agasicles* and *Disonycha argentinensis*. This overall size increase may have developed after various compensating length increases in the vittate ancestral form of the Paraguayan form of *A. opaca*, i.e., when it was a vittate species not far removed from the earlier ancestral form resembling small-sized *Agasicles hygrophila* (fig. 40 between C and D).

Figures 50 through 60 are the bivariate normal ellipses for 11 different sets of character pairs. Each set is composed of a series for the females (A) and a series for the males (B) of five forms of *Agasicles* and the related *Disonycha argentinensis*. In each series, the heavy line connecting the mean points for each species represents, as described earlier, the first-version phenocline, or the estimated evolutionary trend. The sequence of the six species is the same as that given for Recent time in the dendrogram shown in figure 40. For the fasciate *Agasicles opaca* normal ellipses are given only for the combined samples collected in the Paraguay River and in the lower Amazon, 1960–61. Samples collected in 1975 combined with the 1960–61 samples will be considered in the next section.

Even though the configurations of the phenoclines are diverse, in each of 10 of the 11 sets there is remarkable concordance between trends for the females (A) and the males (B), indicating little to no sexual dimorphism. In a single set (fig. 60), however, there is marked discordance, clearly representing the obvious sexual dimorphism that is so

strikingly developed in *Agasicles*. Much less obvious sexual dimorphism is detectable from the graphs for three of the ten remaining sets and is summarized in table 5.

Figure 50 represents the relationship of pronotal width (PrW) to pronotal length (PrL). The ellipses all show rather strong positive intercharacter correlations, there being consistent alignment among them. Clear taxonomic discrimination is apparent in the normal ellipses representing *Disonycha argentinensis* and *Agasicles opaca*.

The phenocline between *Disonycha argentinensis* and *Agasicles hygrophila* shows a marked reduction in width and a moderate increase in length. Between *A. hygrophila* and *A. opaca* there is a general increase in length and width, with the mean points for the vittate species rather closely clustered. The considerably smaller size of *A. hygrophila*, the only species ranging into a temperate climate, is also evident in figures 51 and 52 with respect to body (elytral) width, body length, and body thickness. The smaller size might seem to be related to restrictive growth conditions besetting alligatorweed during summer, late fall, and winter. These temperate-climate conditions might seem to be most pronounced in their effects on alligatorweed regenerating from attack by *Agasicles*. However, we have no consistent evidence that shows geographical differences in alligatorweed regeneration in South America. Nor do we have any evidence that *Agasicles hygrophila* is any more suppressive of alligatorweed than any of its vittate allopatric congeners. Also, as already pointed out, *A. vittata*, a species of intermediate size, is limited to *Alternanthera sessilis* over part of its range. This amphibious amaranth is the one with the most slender stems, *A. reineckii* excepted. Therefore, the small size of *Agasicles hygrophila* remains an enigma unless it is a manifestation of relationship to the similar-sized, closest extrageneric relative, *Disonycha argentinensis*. If true, we can extend this explanation to account for the progressive increases in size from *A. hygrophila* to *A. connexa* to *A. interrogationis* and *A. hygrophila* to *A. vittata* (figs. 50–52).

On the other hand, the great size increase of *Agasicles opaca* is more clearly attributable to the large stem cavity of its host plant, *Alternanthera hassleriana* (figs. 50–52). In contrast with the vittate species that are clearly limited in size by stem diameters of *A. sessilis* and by alligatorweed, the forms of *Agasicles opaca* consistently have space to spare for pupation in the internode of *Alter-*

nanthera hassleriana (fig. 49). However, when the fasciate forms pupate in alligatorweed, stem-size limitation must come into play to limit flea beetle size. It may be significant that our experience with the Amazonian *Agasicles opaca* shows much less association with alligatorweed (almost none) than does the Paraguay River form. This difference may relate to the smaller size of the Paraguayan form as compared with Amazonian fasciate forms and reflect restrictive stem size being imposed by alligatorweed. The size of the Paraguayan and Amazonian forms of *A. opaca* will be taken up in the next section.

Figure 51 represents the relationship of elytral length (EL) to elytral, or body, width (EW). Being consistently alined, the ellipses show strong inter-character correlations, which are positive in all cases. There is more range of variation longitudinally than transversely to the body axis. Except for the combined fasciate *Agasicles* forms, the normal ellipses show no clear taxonomic discrimination between the species of *Agasicles*.

From soil-pupating *Disonycha argentinensis*, the phenocline shows a significant although small decrease in elytral width, with little change in length, a reduction presumably permitting better fit of *Agasicles hygrophila* inside the host-plant stem. As flea beetle size increases, elytral length increases more than width, with the greatest increase in width and length being attained by the combined *A. opaca* forms of *Alternanthera hassleriana*. Note the extent of the steep slope of the trend between the large fasciate species and the smaller vittate species.

Across the elytra (elytral width) is the widest portion of the adult body. But the elytra are wrapped around the body of the pupa and are actually exceeded laterally by the apices of the projecting rigid femora (figs. 22 and 23). The elytra are among the last body parts to be extended and sclerotized during and after ecdysis. They remain in a pliable condition while the newly emerged, unfed, and still not full-sized adult remains inside the stem. In the adult the elytra enclose the pterothorax and abdomen that in turn house the large flight muscles and the space-demanding ovaries. The ratio of width to thickness to length of body can only undergo limited adjustment without seriously interfering with the flea beetles' jumping ability to avoid danger. Already, slenderization of body and appendages seems to have rendered *Agasicles* less agile than its disonychine relatives. Therefore, elytral width probably can undergo

only limited reduction and is considered to be a less sensitive measure of constrictive effects of the host-plant stem than is the pronotum.

Figure 52 represents the relationship of body length (TBL) to body thickness (BTh). Again consistently alined, the ellipses show strong inter-character correlation. Except for the combined *Agasicles opaca* forms, they show no clear taxonomic discrimination among the species.

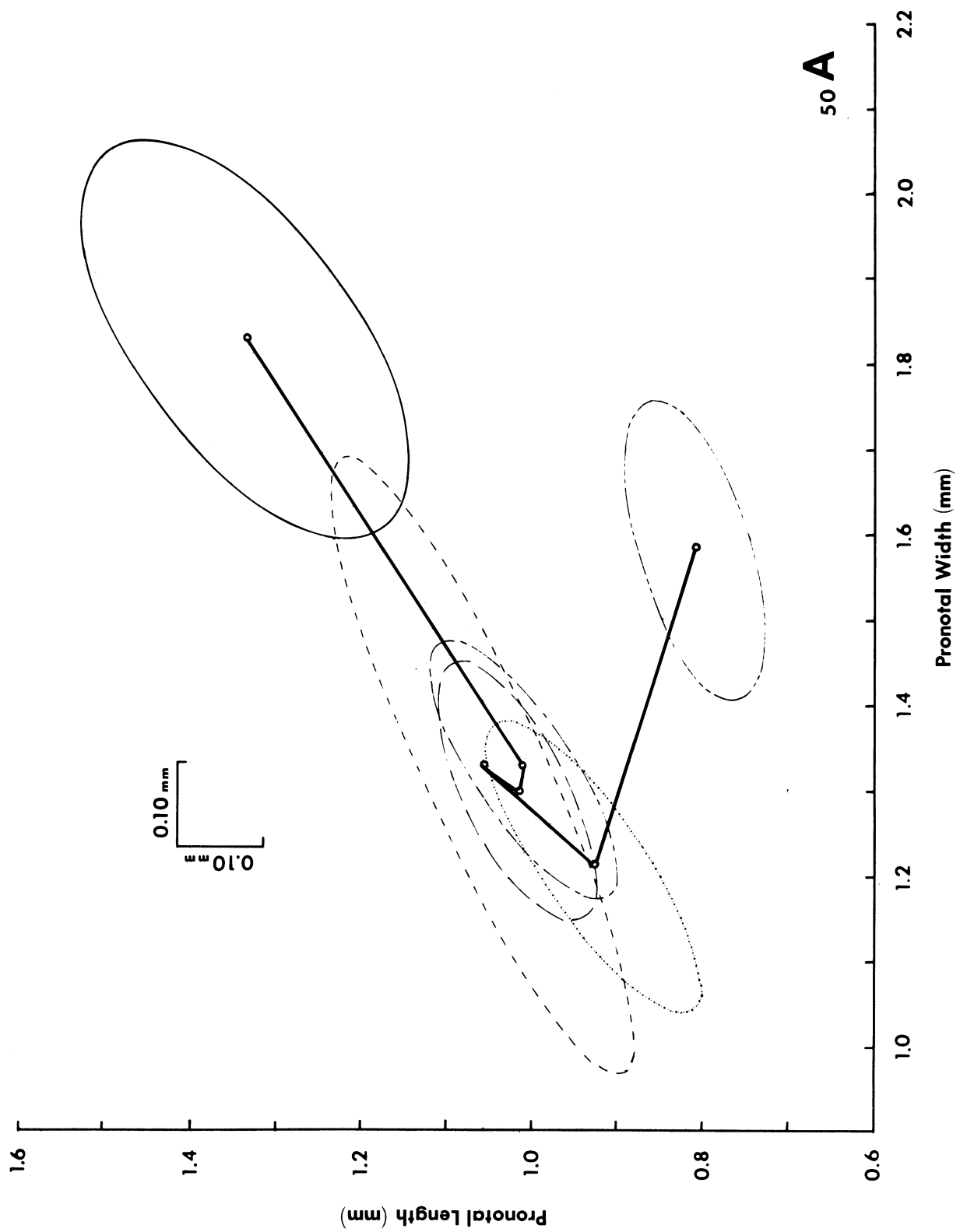
The phenocline approaches a straight line with little separation between *Disonycha argentinensis* and *Agasicles hygrophila*. The slope of the phenocline represents a gradual size increase. As indicated in the previous discussion, width as well as length has control over body thickness. Accordingly, as flea beetle size increases, length of body increases more than thickness of body, with the greatest increases being attained by *Agasicles opaca*. This progressive differential rate of increase is also more or less evident in figures 51 and 55-60 and indicates clearly a consistent tendency in *Agasicles* to increase in size. The progression corresponds with increasingly tropical climates on one hand and increasing distance from the range of *Agasicles hygrophila* on the other. It may also correspond with an increase in host-plant stem diameter in some way not presently recognized. Both figures 51 and 52 show a discontinuity in the trend between *A. interrogationis* and *A. vittata*. This will reappear in figures 55, 56, and 58.

Figure 53 represents the relationship of head width (HW) to head length (HL). The ellipses are variously oriented, with the two for the female *Agasicles connexa* and *A. interrogationis* having negative coefficients of correlation. But even so, no clear taxonomic discrimination is evident among species.

The mean points of the ellipses are rather closely clustered; and although the head width of adult and pupa are less than the pronotal width (figs. 1-6 and 21-23), head width is significantly reduced in the phenocline from *Disonycha argentinensis* to *Agasicles hygrophila*. As body size increases, head size fluctuates in a narrow range from *A. hygrophila* through the vittate species and then markedly to the combined forms of *A. opaca*. Head length shows less change than width over most of the phenocline.

Figure 54 represents the relationship of interocular width (IOW) to interantennal width (IAW). The ellipses are rather consistently alined, with all coefficients of correlation positive. Except for the com-

(Continued on page 74.)



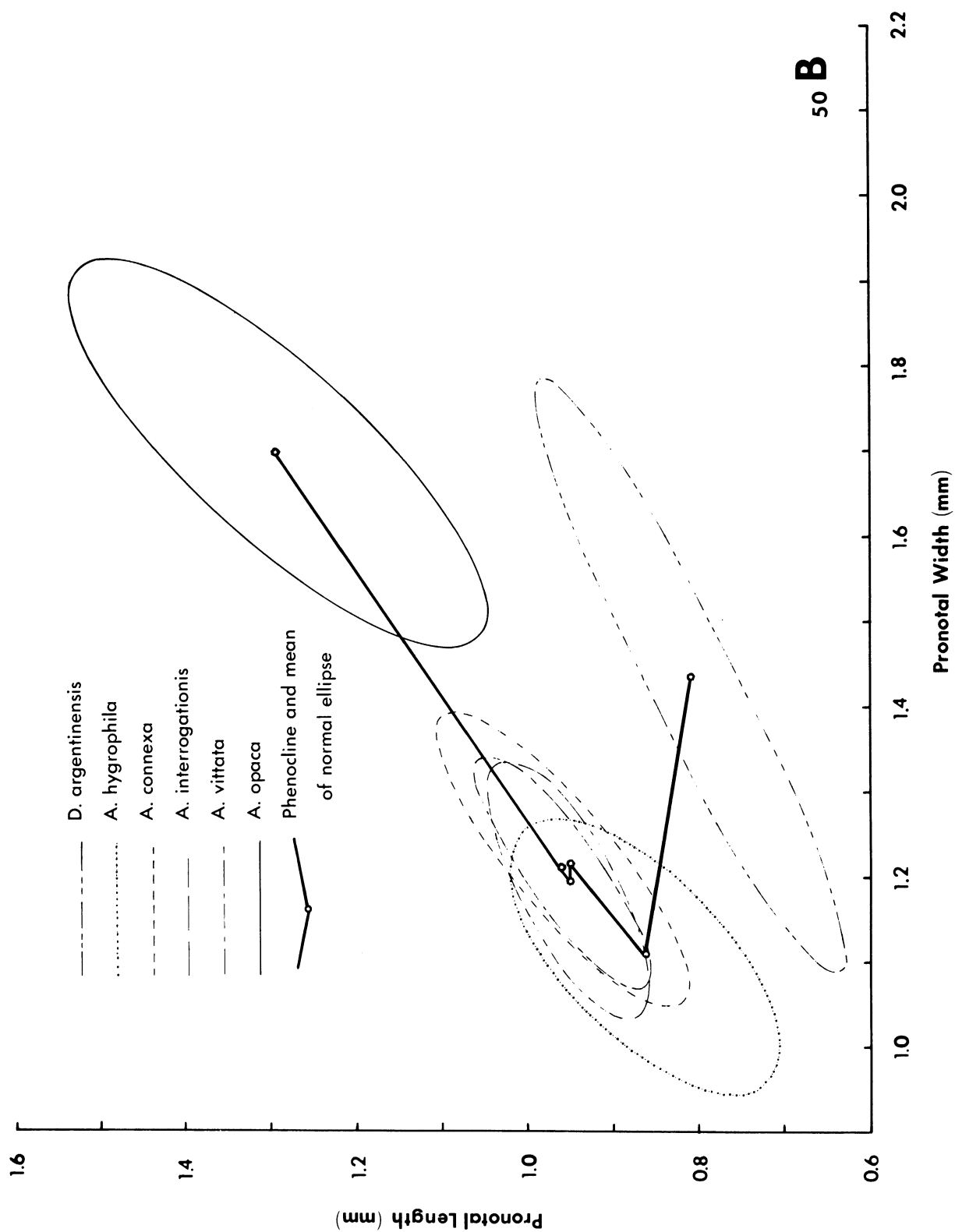
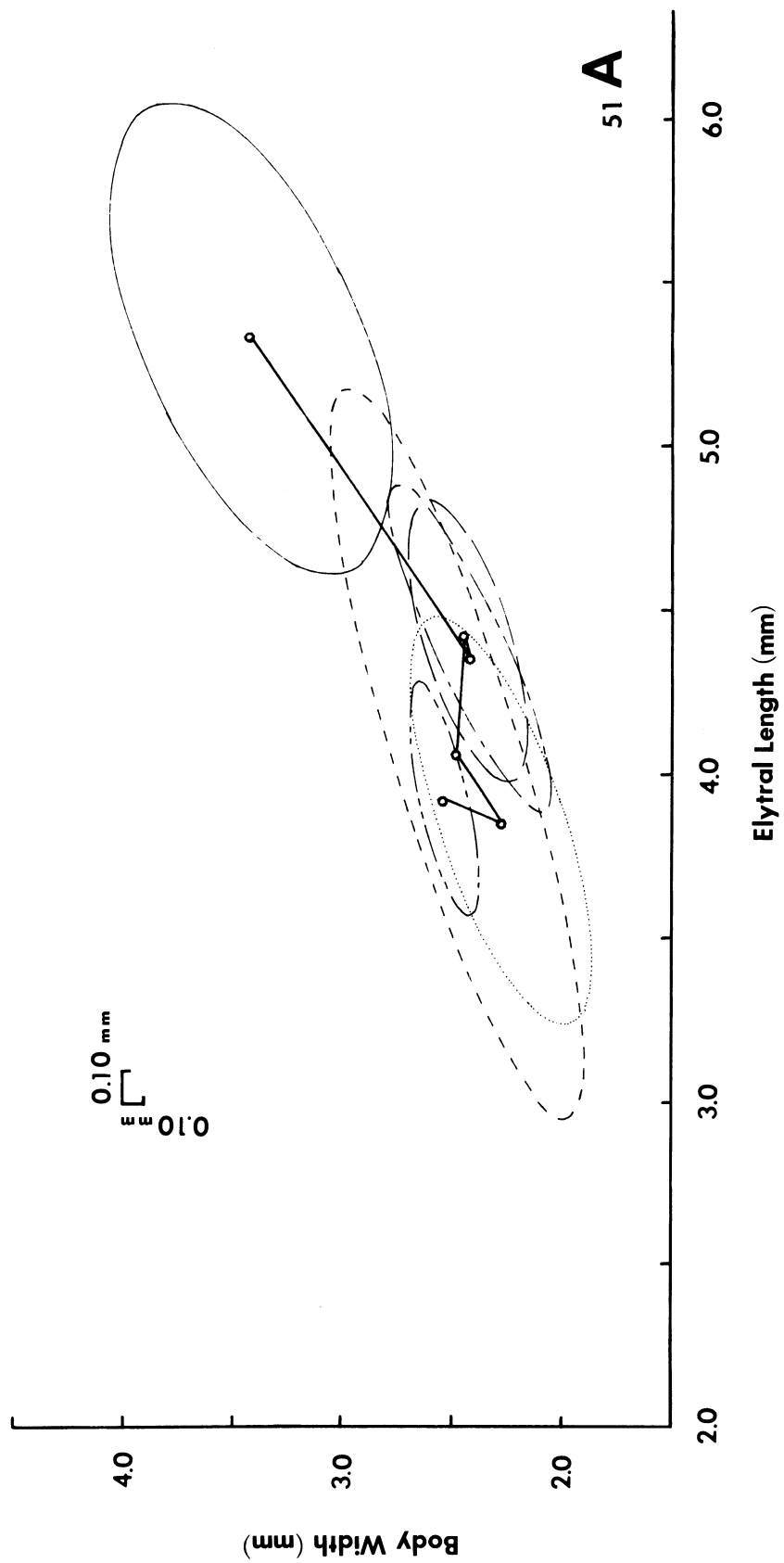


FIGURE 50.—Means and bivariate normal ellipses (first version) for relations in flea beetles between pronotal width and length. A, Females. B, Males. Paraguayan and Amazonian forms of *Agasicles opaca* are combined.



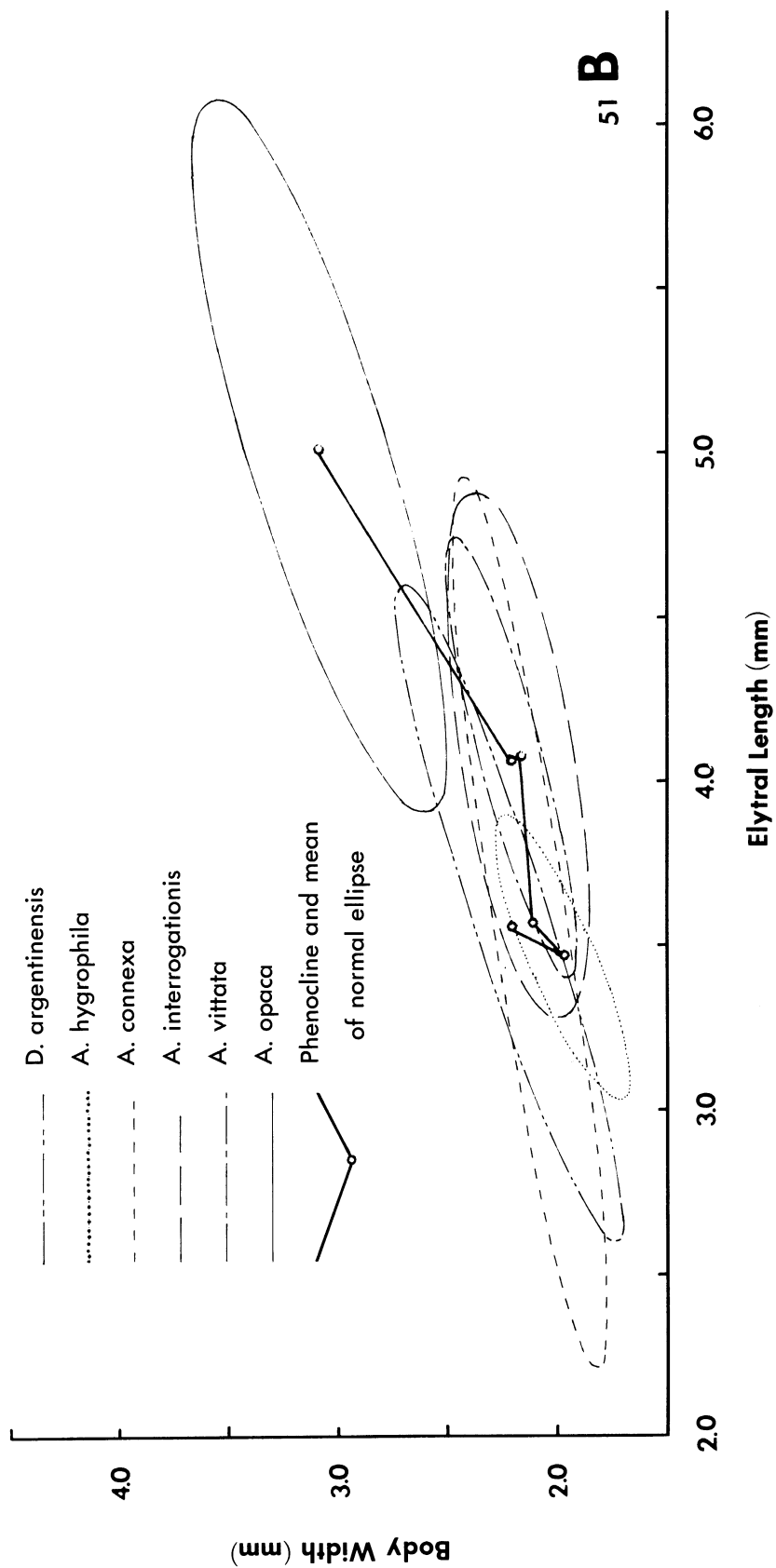
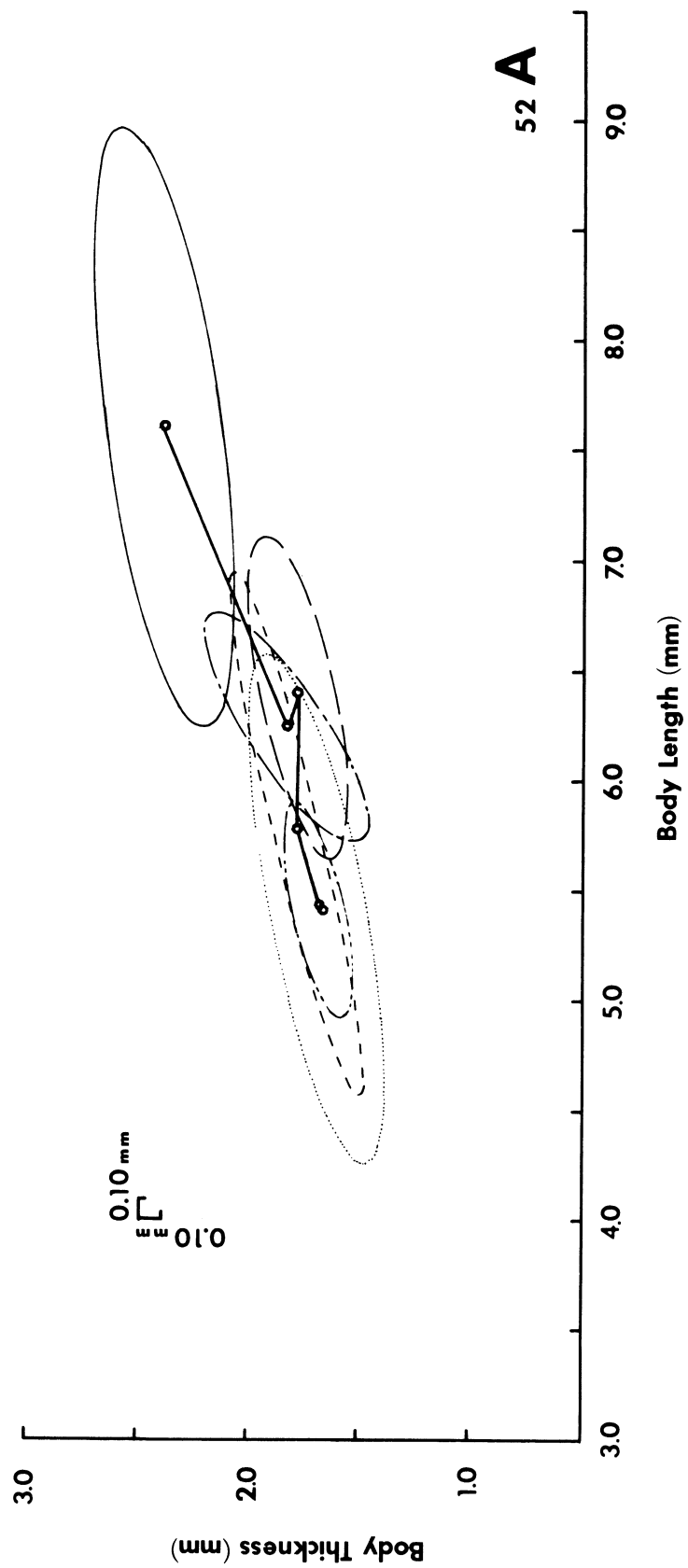


FIGURE 51.—Means and bivariate normal ellipses (first version) for relations in flea beetles between elytral length and width. A, Females. B, Males. Paraguayan and Amazonian forms of *Agasicles opaca* are combined.



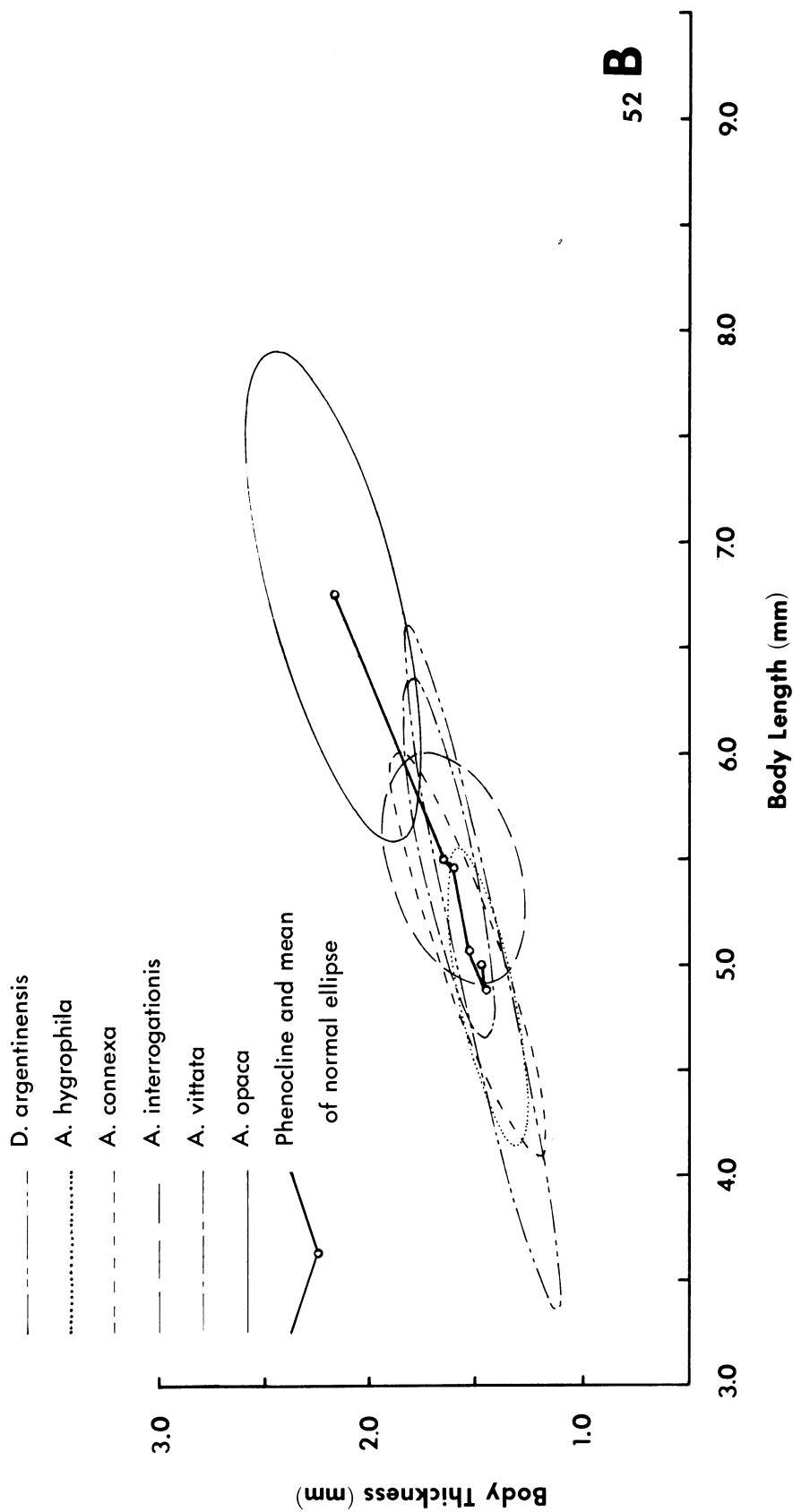
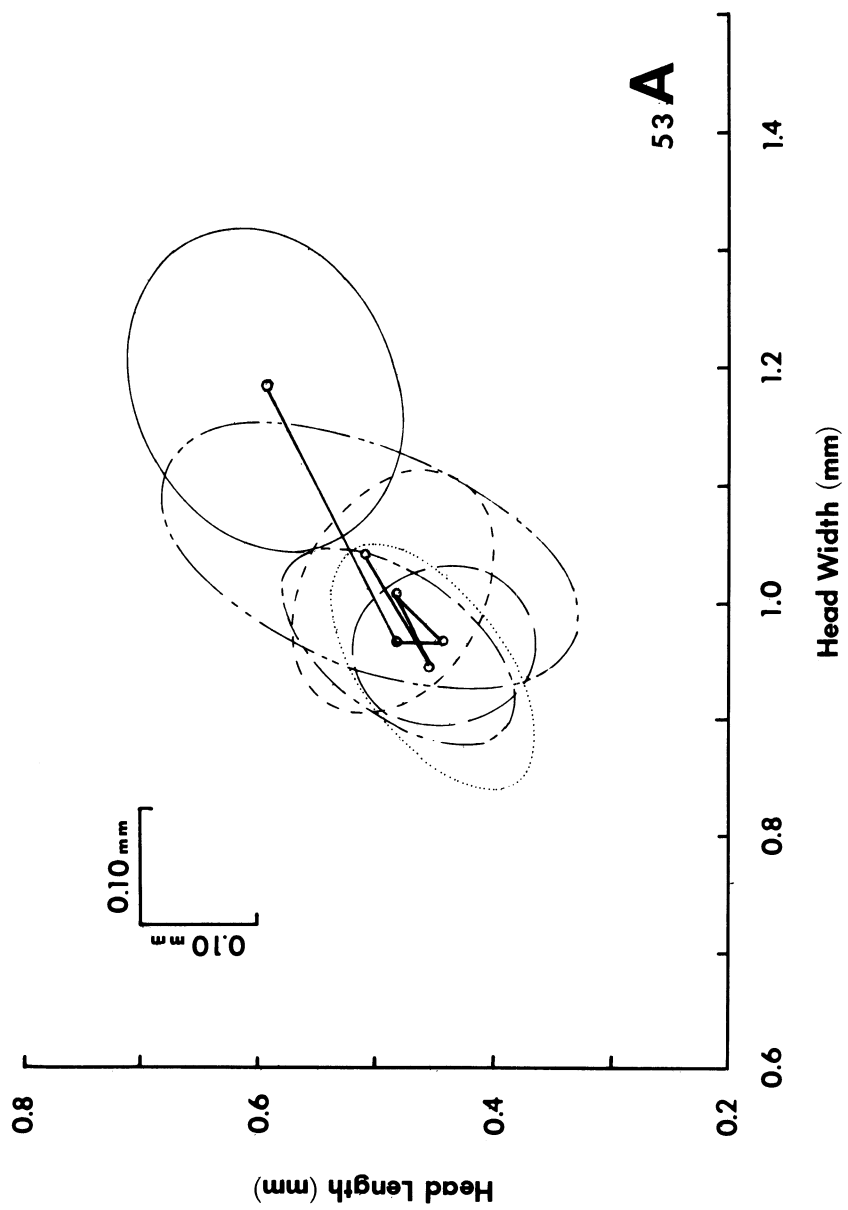


FIGURE 52.—Means and bivariate normal ellipses (first version) for relations in flea beetles between total body length and thickness. A, Females. B, Males. Paraguayan and Amazonian forms of *Agasicles opaca* are combined.



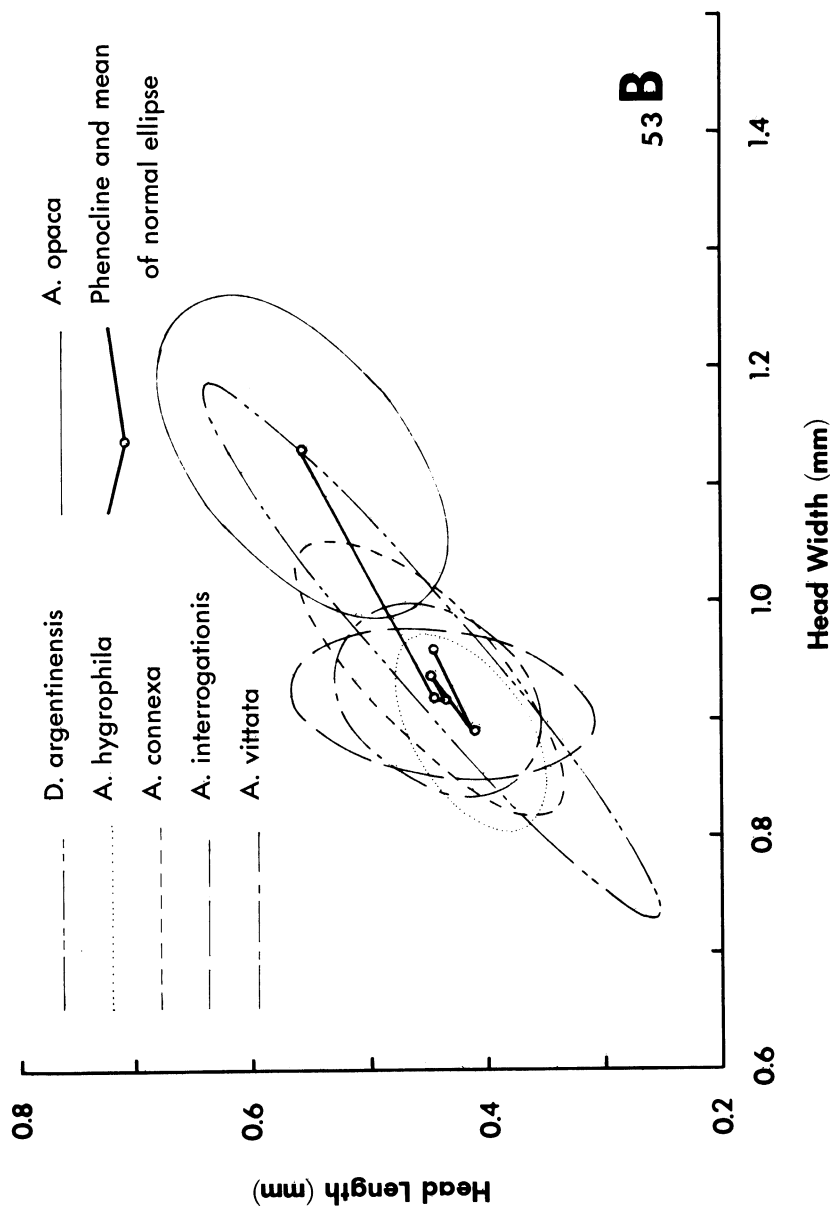


FIGURE 53.—Means and bivariate normal ellipses (first version) for relations in flea beetles between head width and length. A, Females. B, Males. Paraguayan and Amazonian forms of *Agasicles opaca* are combined.

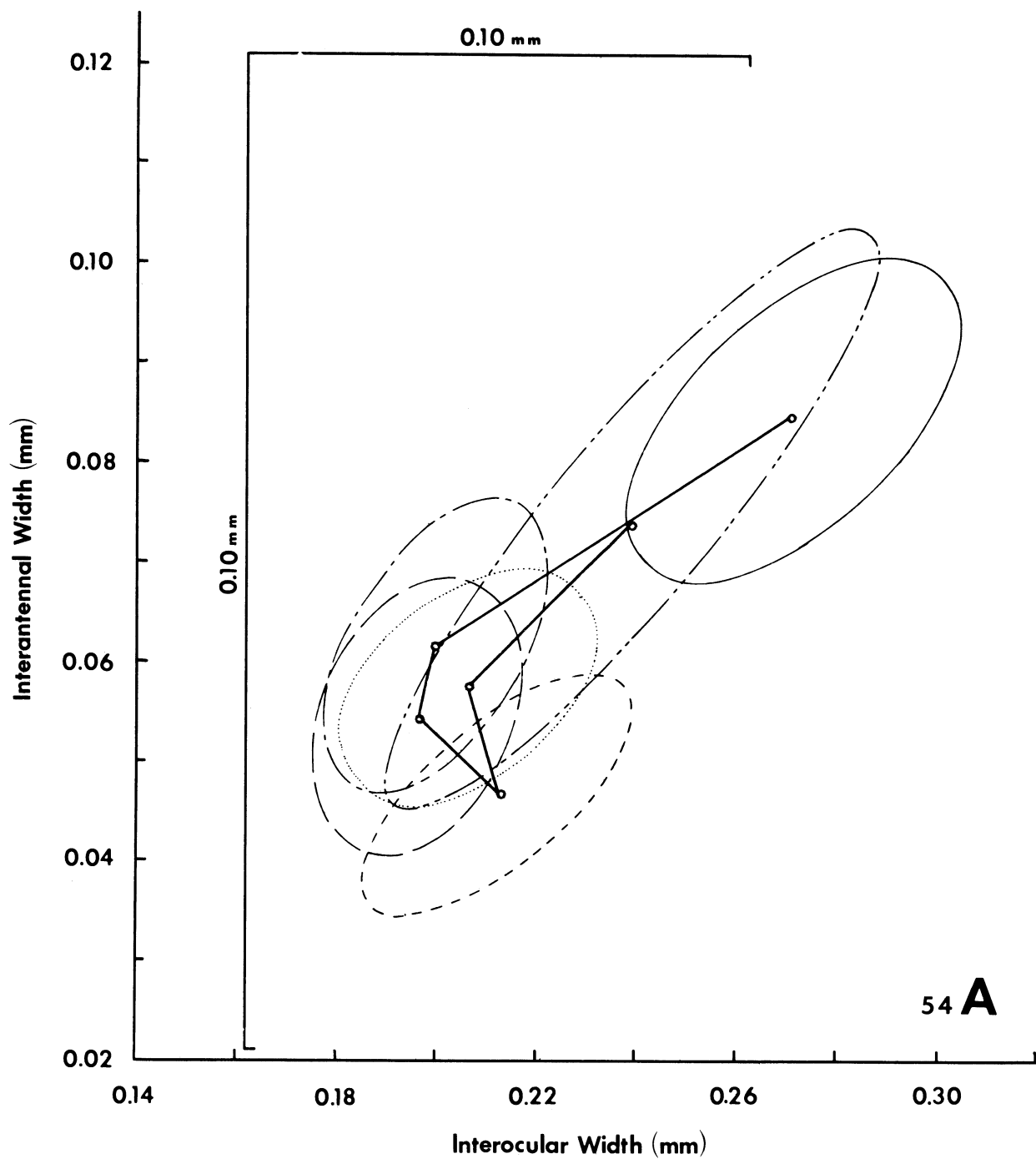
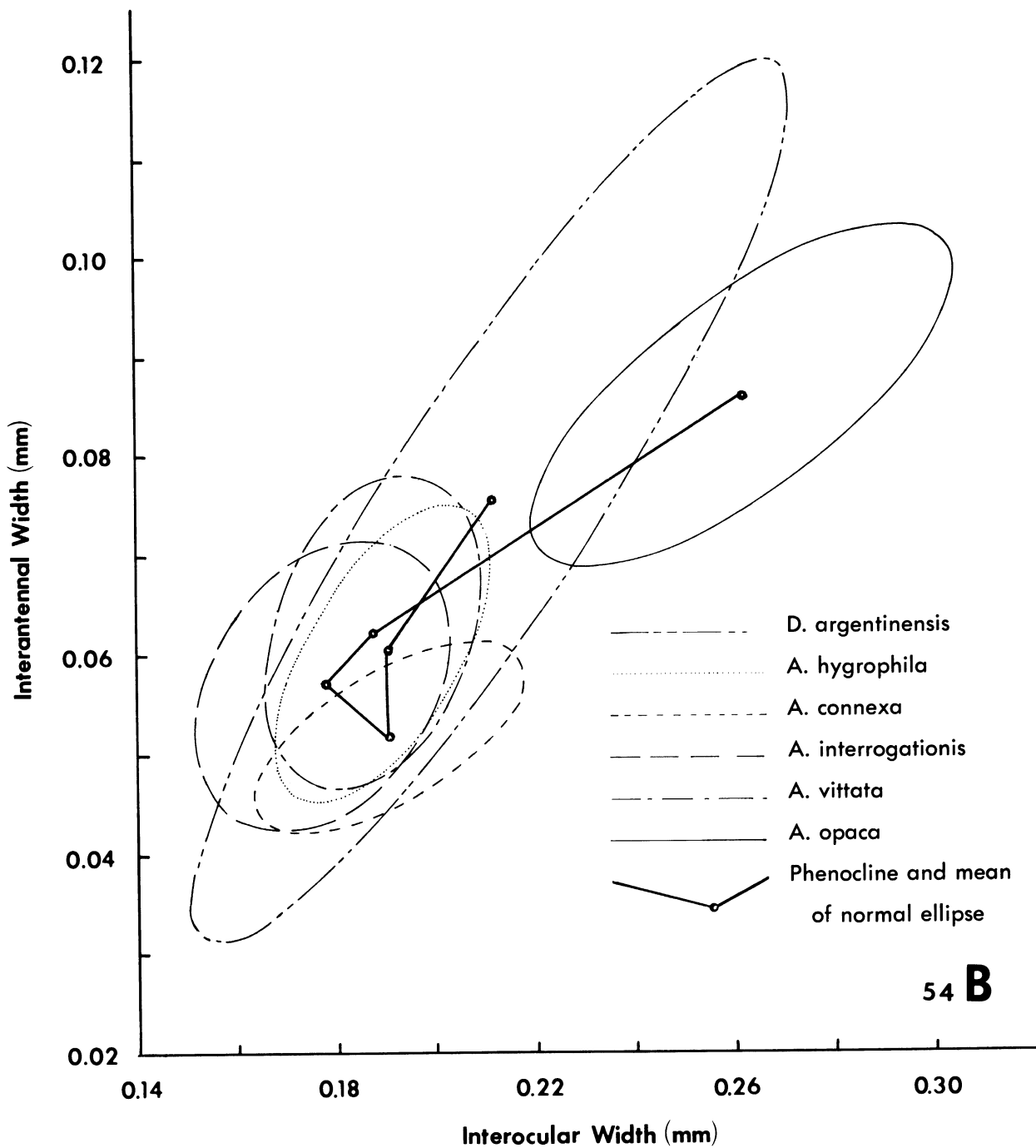
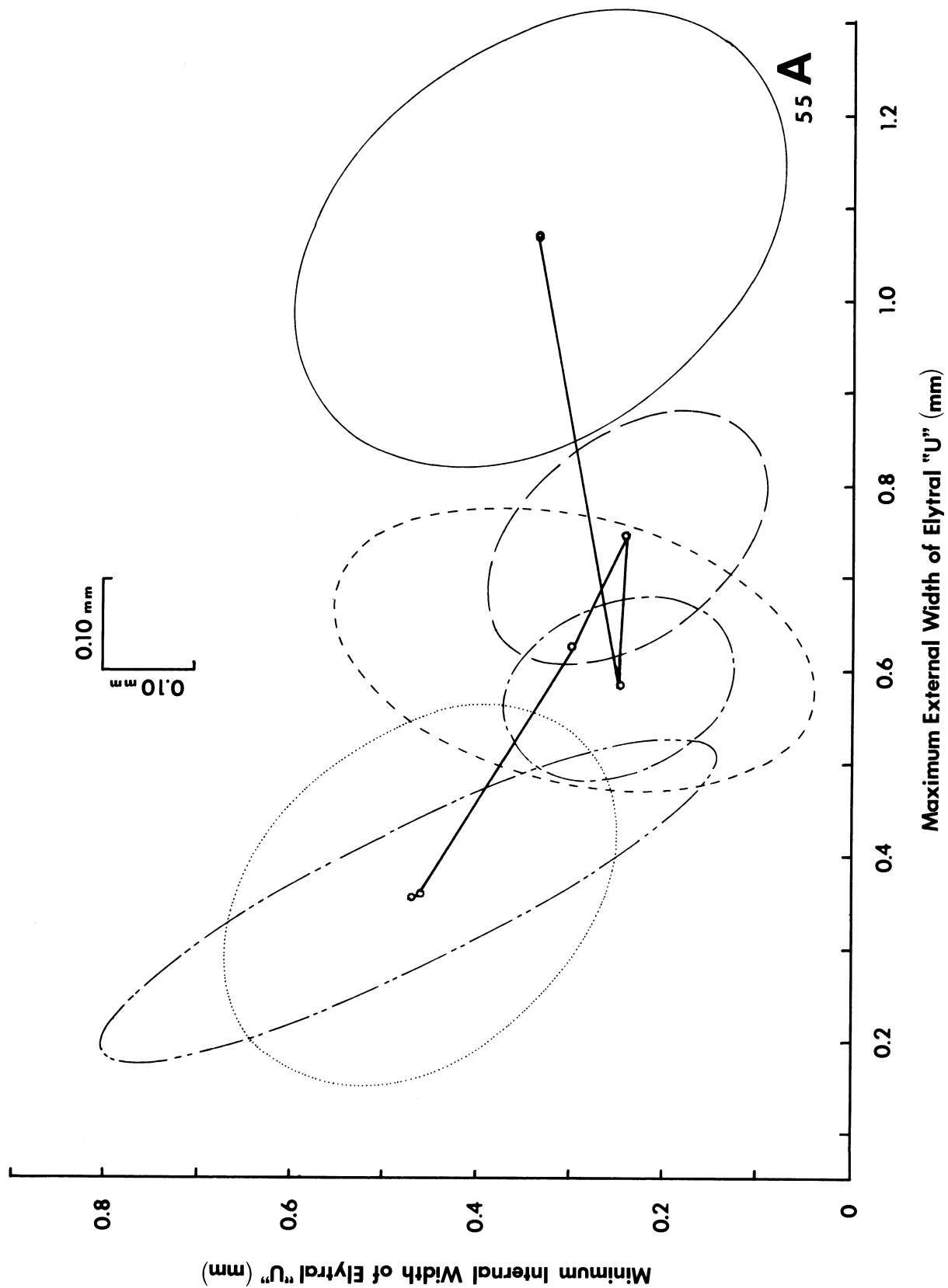


FIGURE 54.—Means and bivariate normal ellipses (first version) for
nal width. A, Females. B, Males. Paraguayan and



relations in flea beetles between interocular width and interanten-
Amazonian forms of *Agasicles opaca* are combined.



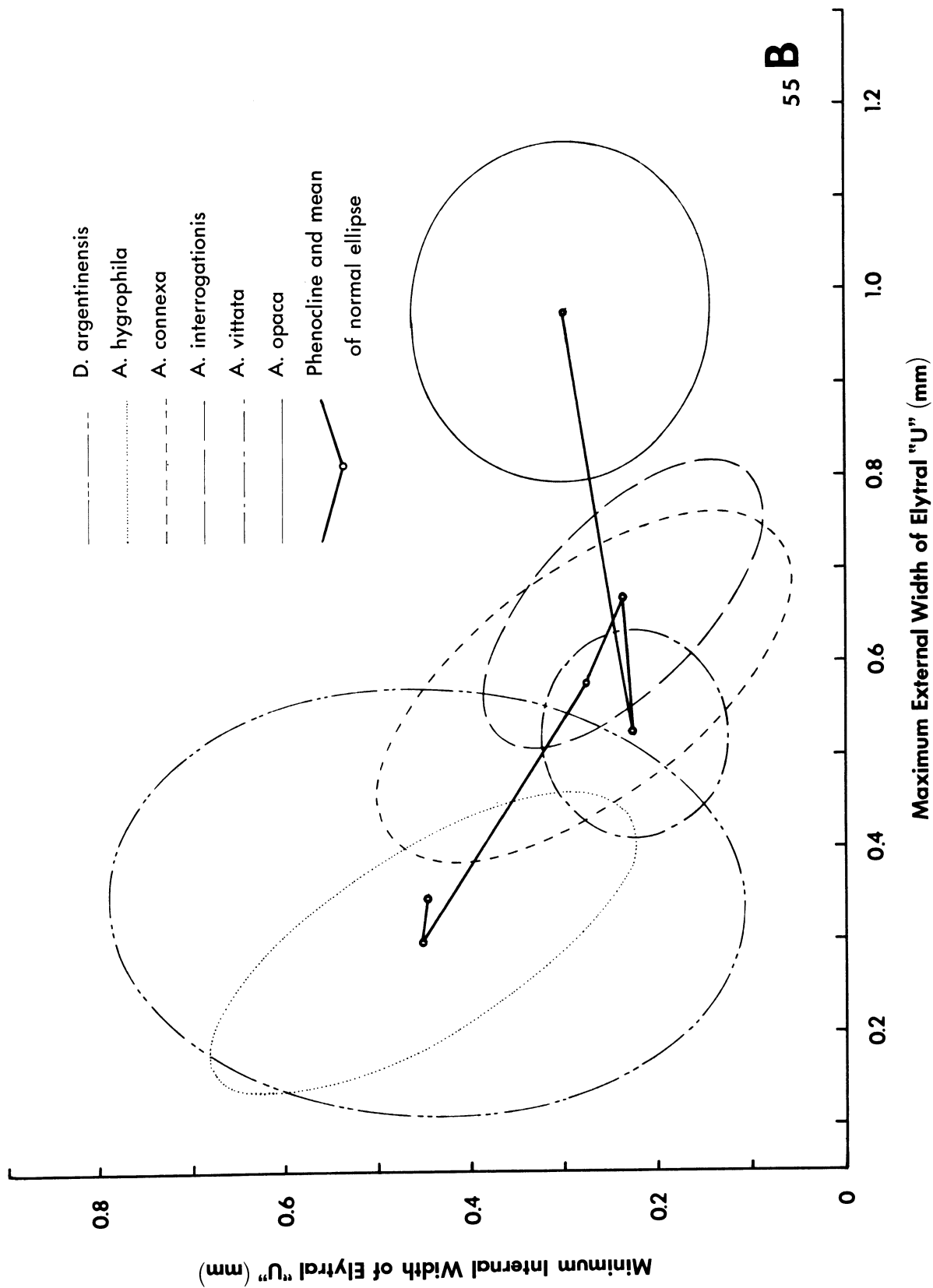
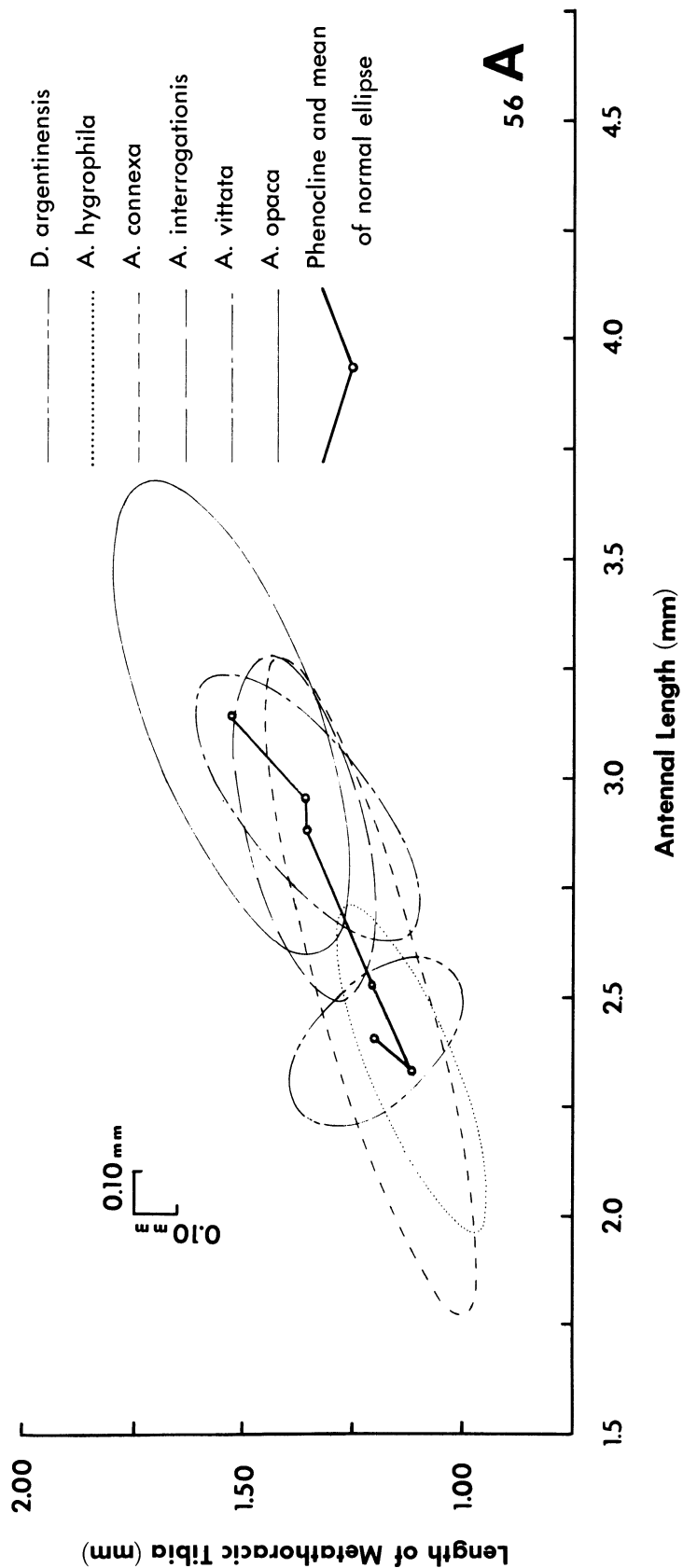


FIGURE 55.—Means and bivariate normal ellipses (first version) for relations in flea beetles between maximum width of the base of the black U-shaped elytral marking and the minimum width of the base of the ivory U-shaped elytral marking. A, Females. B, Males. Paraguayan and Amazonian forms of *Agasicles opaca* are combined.



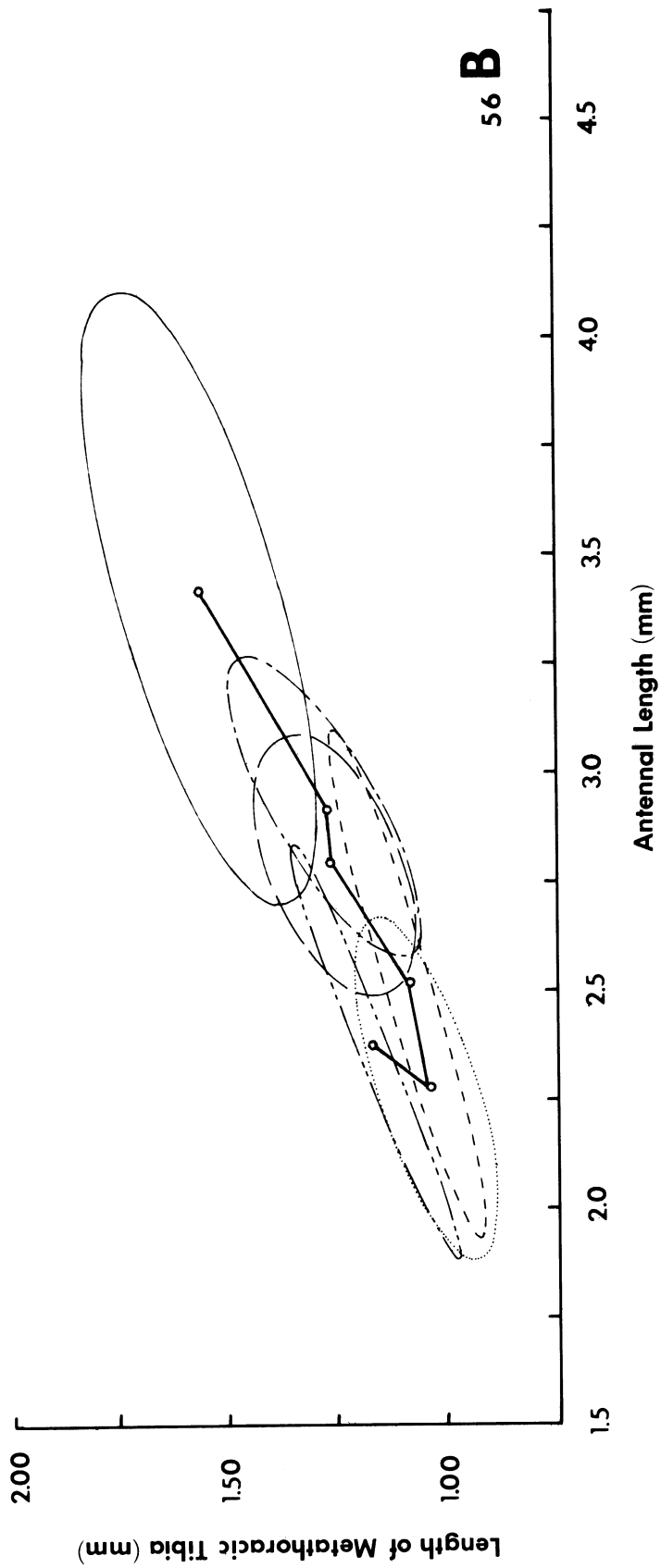
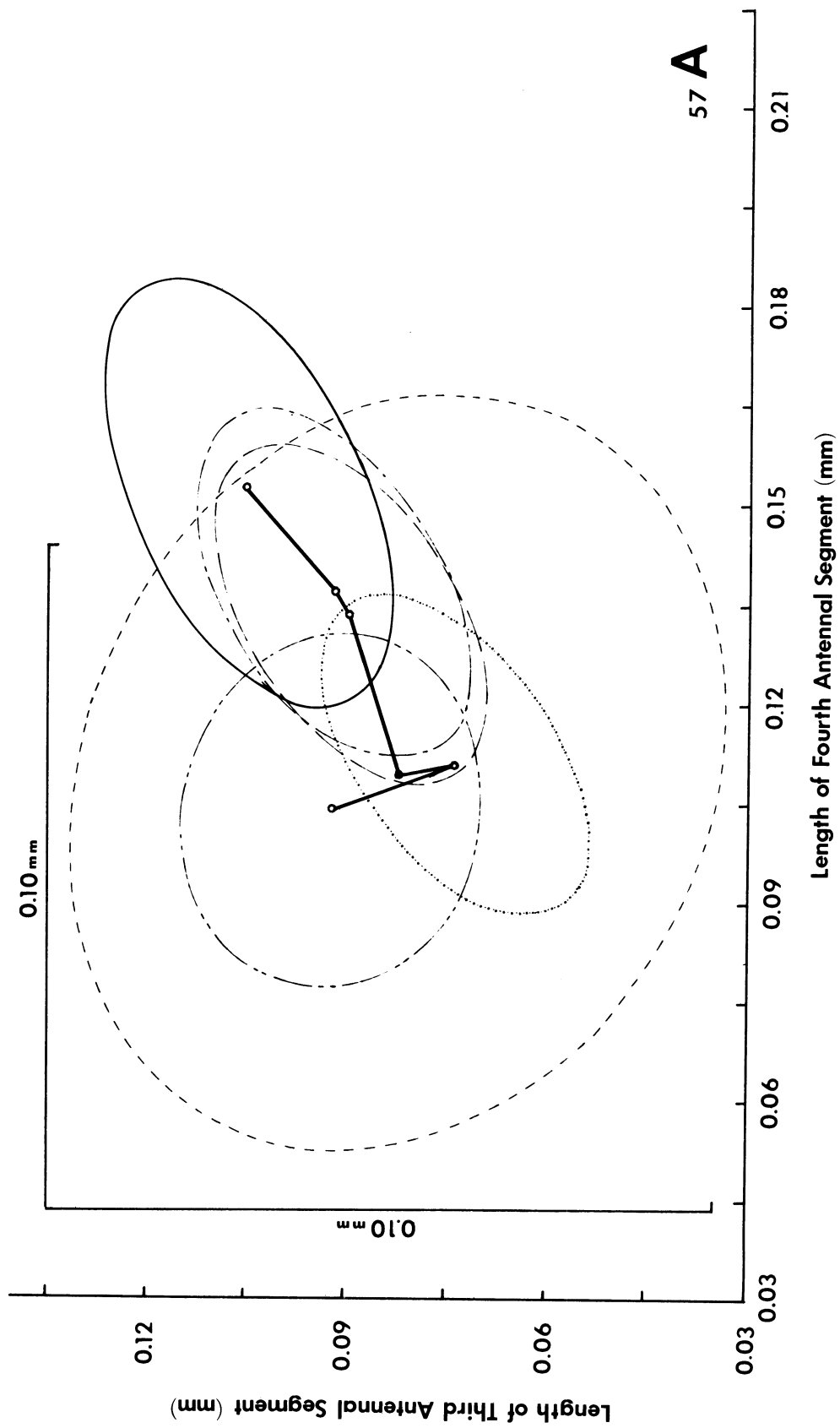


FIGURE 56.—Means and bivariate normal ellipses (first version) for relations in flea beetles between antennal length and metathoracic tibial length. A, Females. B, Males. Paraguayan and Amazonian forms of *Agasicles opaca* are combined.



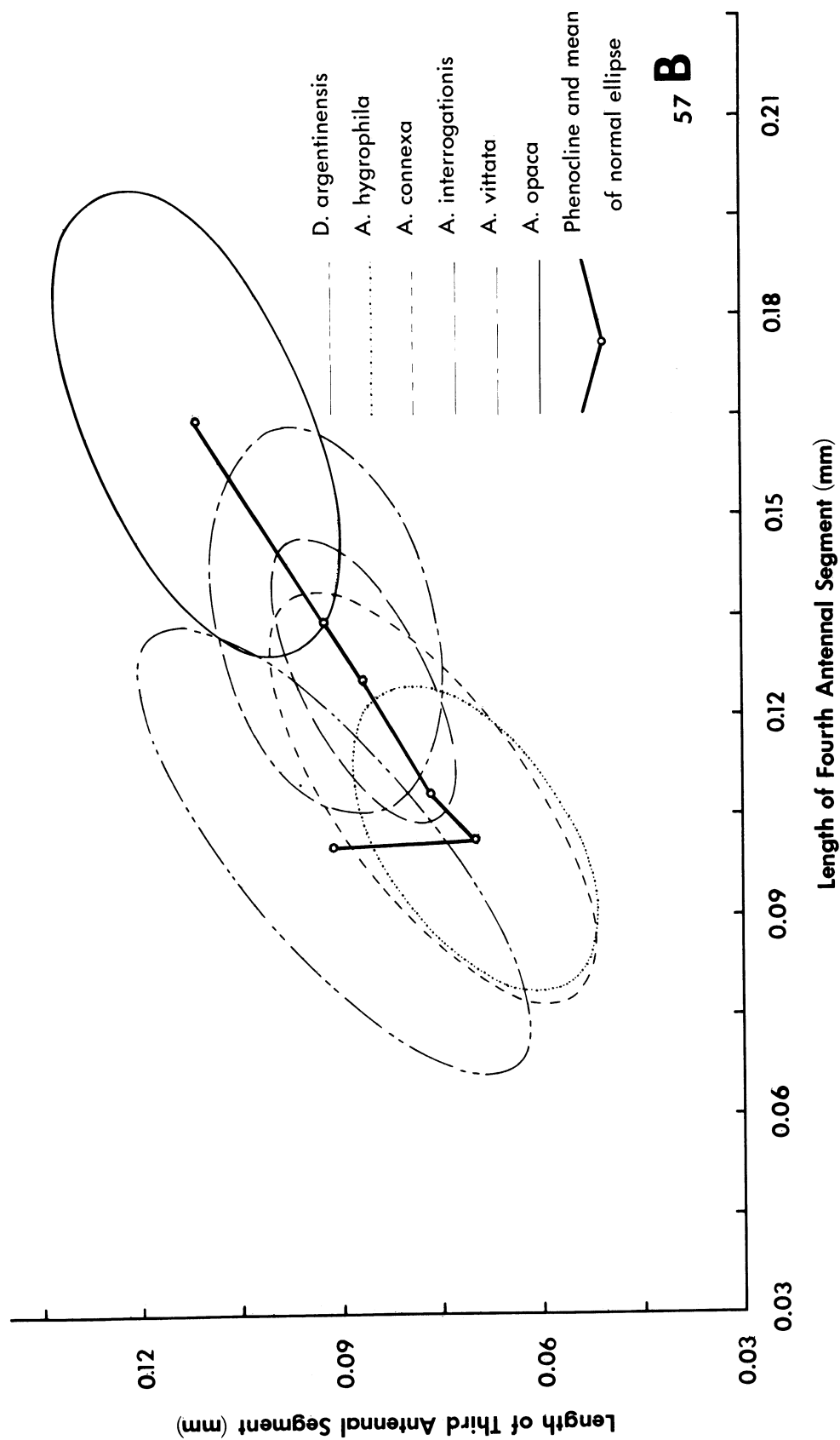
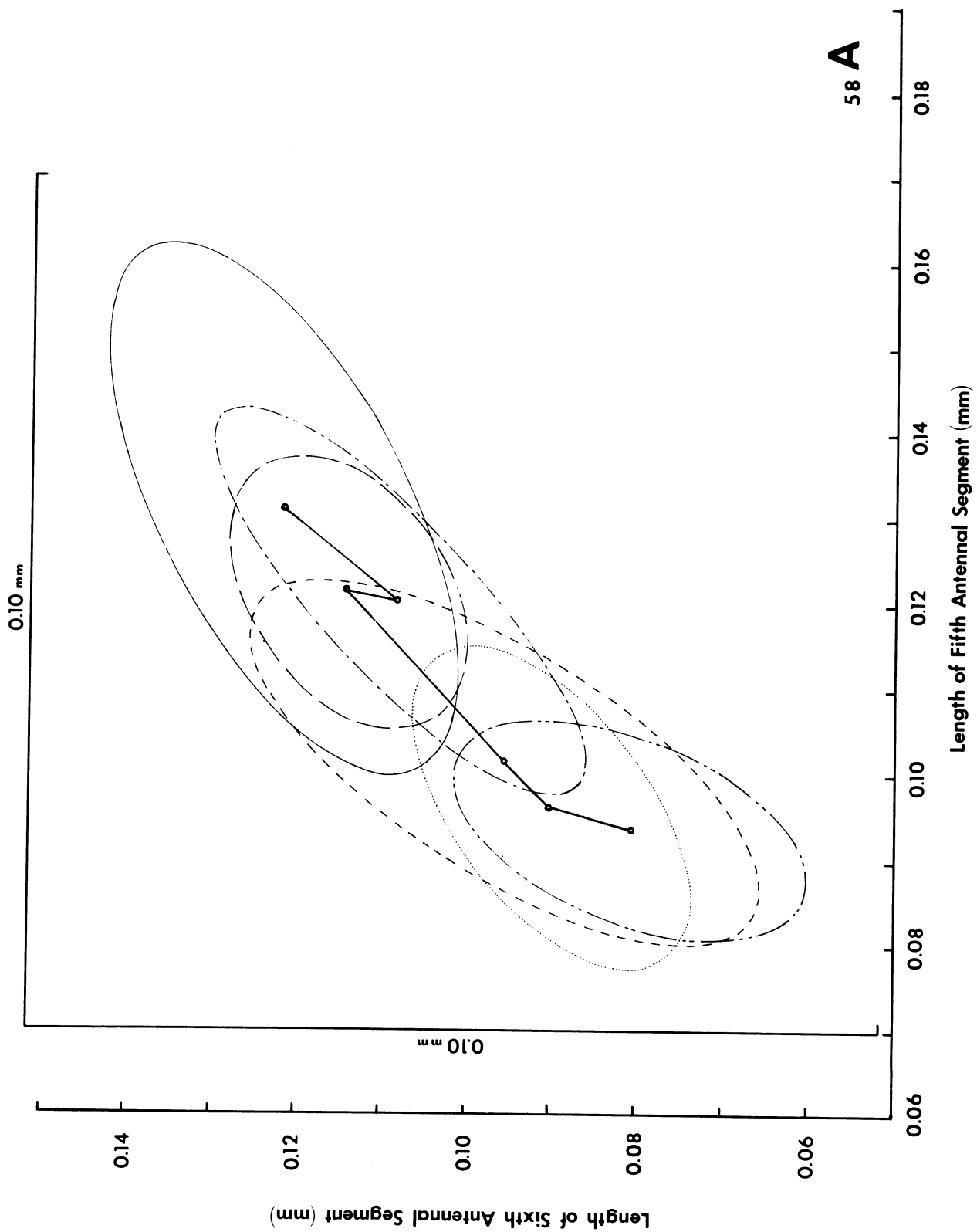
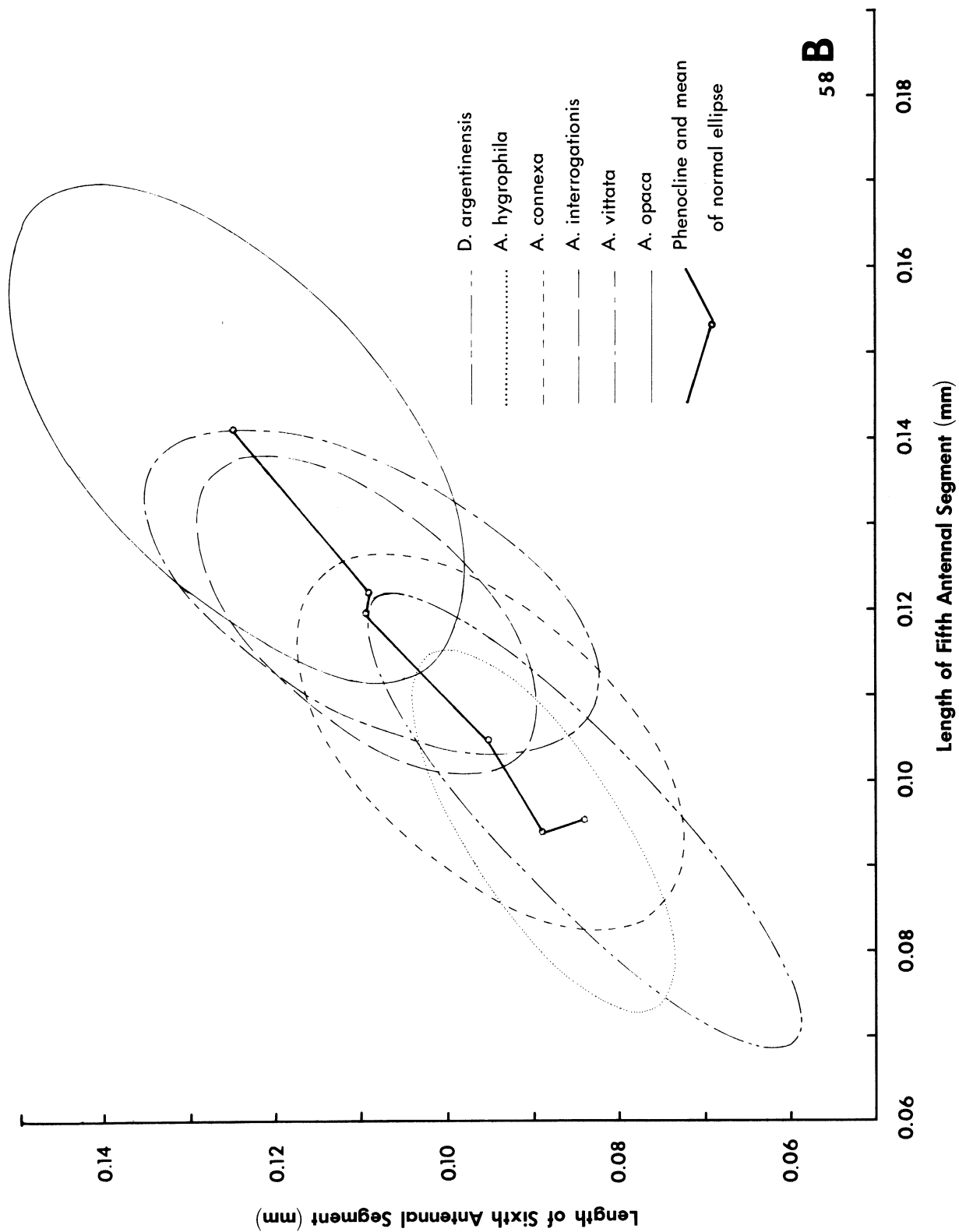


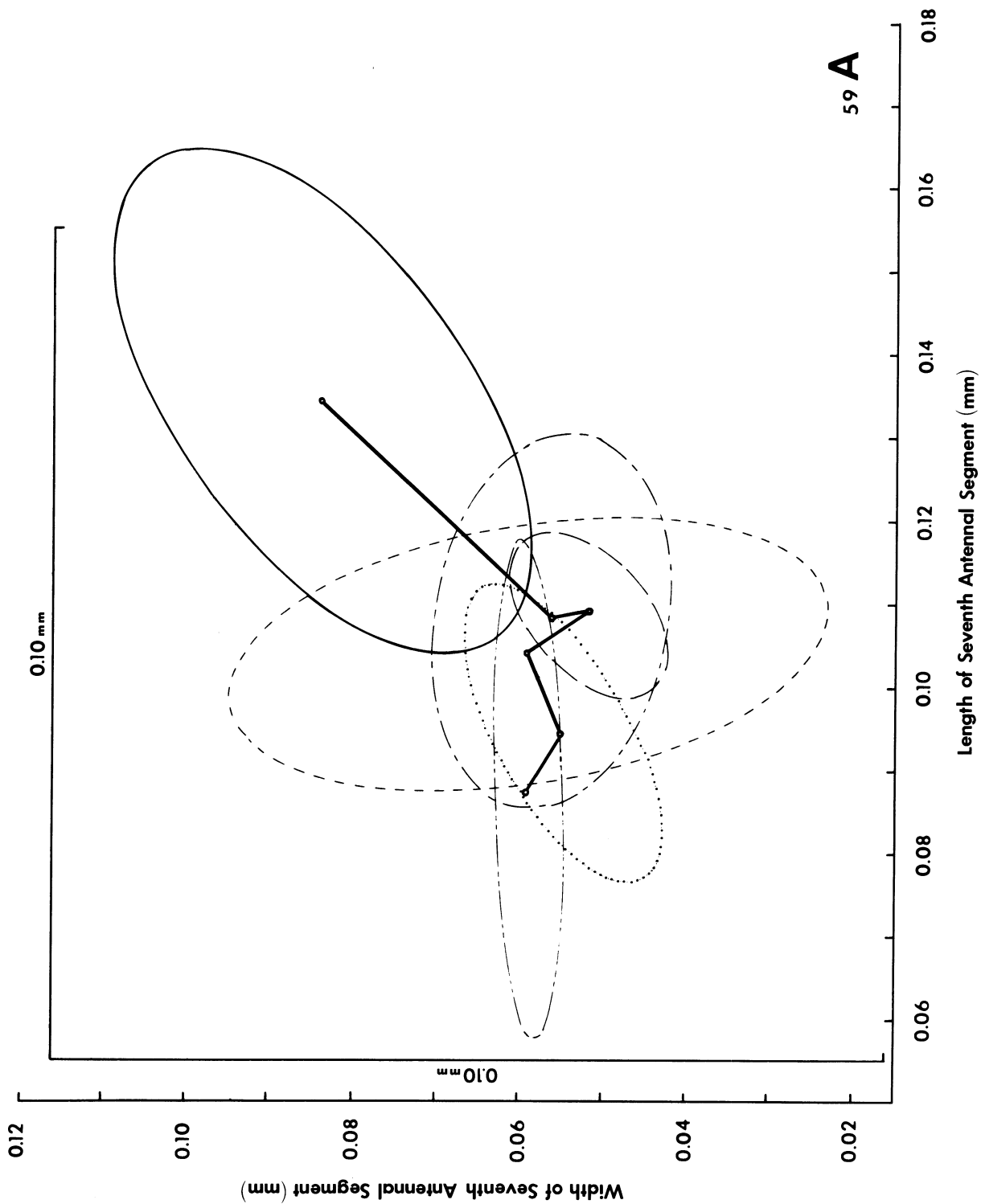
FIGURE 57.—Means and bivariate normal ellipses (first version) for relations in flea beetles between lengths of fourth and third antennal segments. A, Females. B, Males. Paraguayan and Amazonian forms of *Agasicles opaca* are combined.





58 B

FIGURE 58.—Means and bivariate normal ellipses (first version) for relations in flea beetles between lengths of sixth and fifth antennal segments. A, Females. B, Males. Paraguayan and Amazonian forms of *Agasicles opaca* are combined.



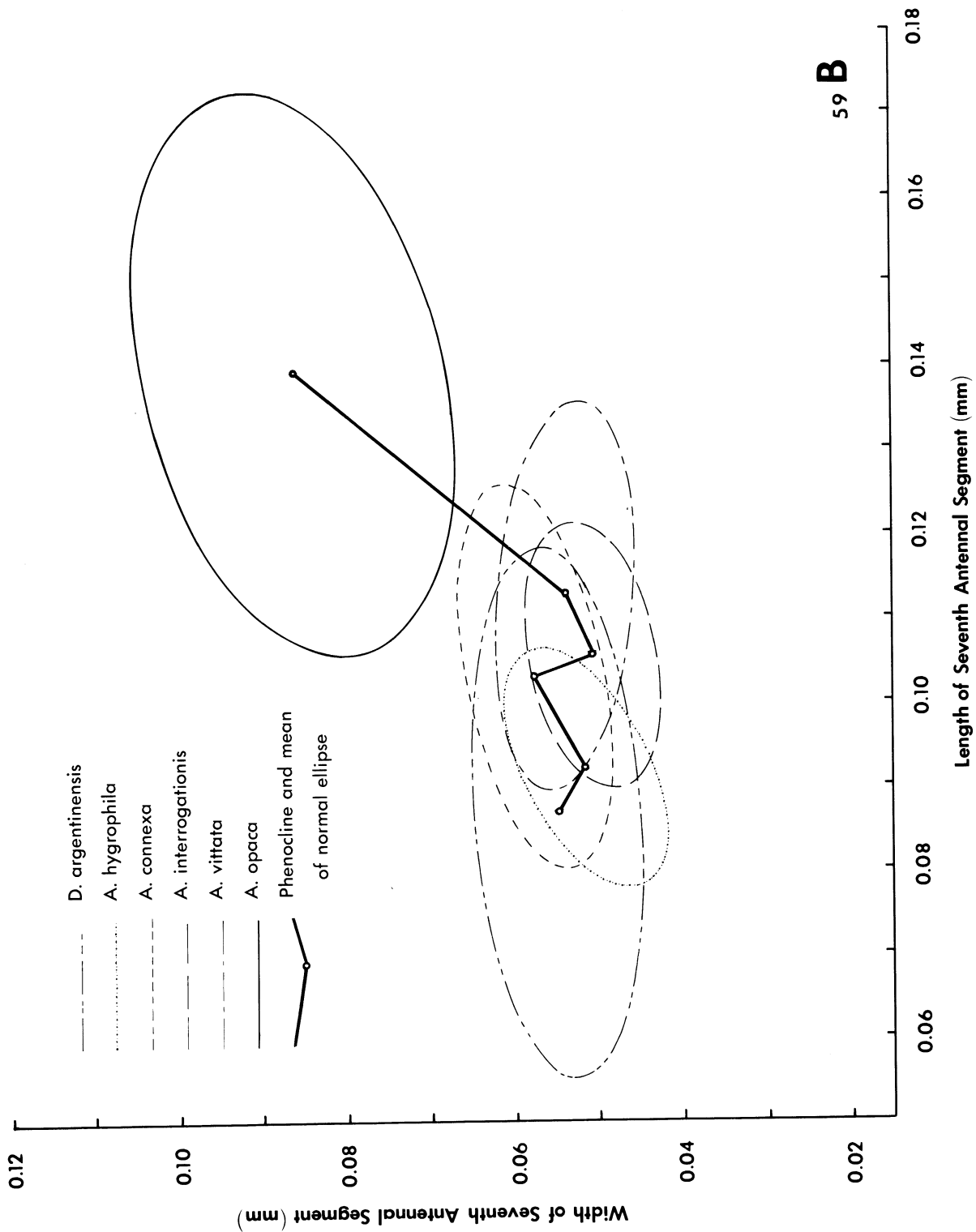
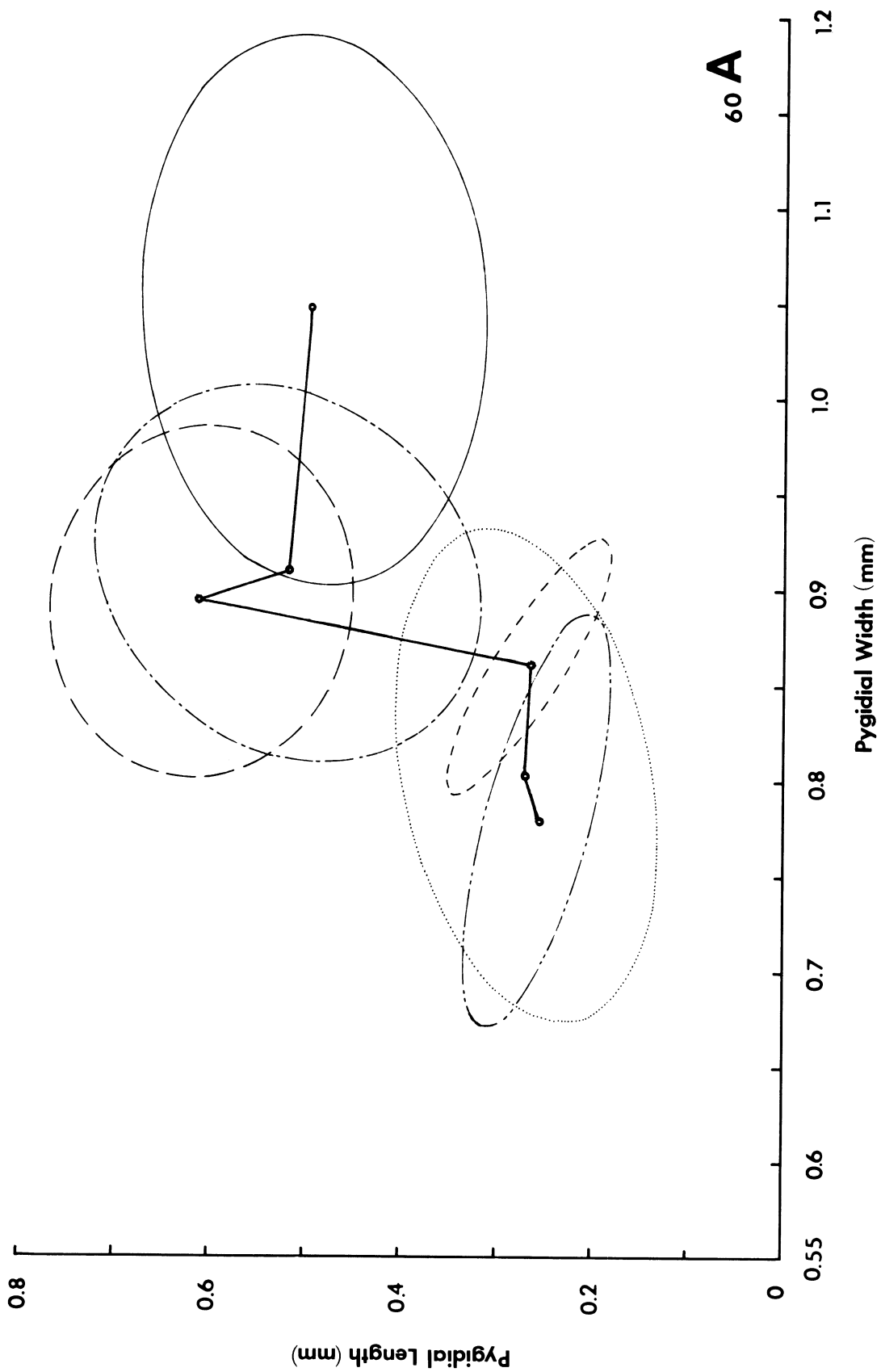


FIGURE 59.—Means and bivariate normal ellipses (first version) for relations in flea beetles between length and width of seventh antennal segment. A, Females. B, Males. Paraguayan and Amazonian forms of *Agasticles opaca* are combined.



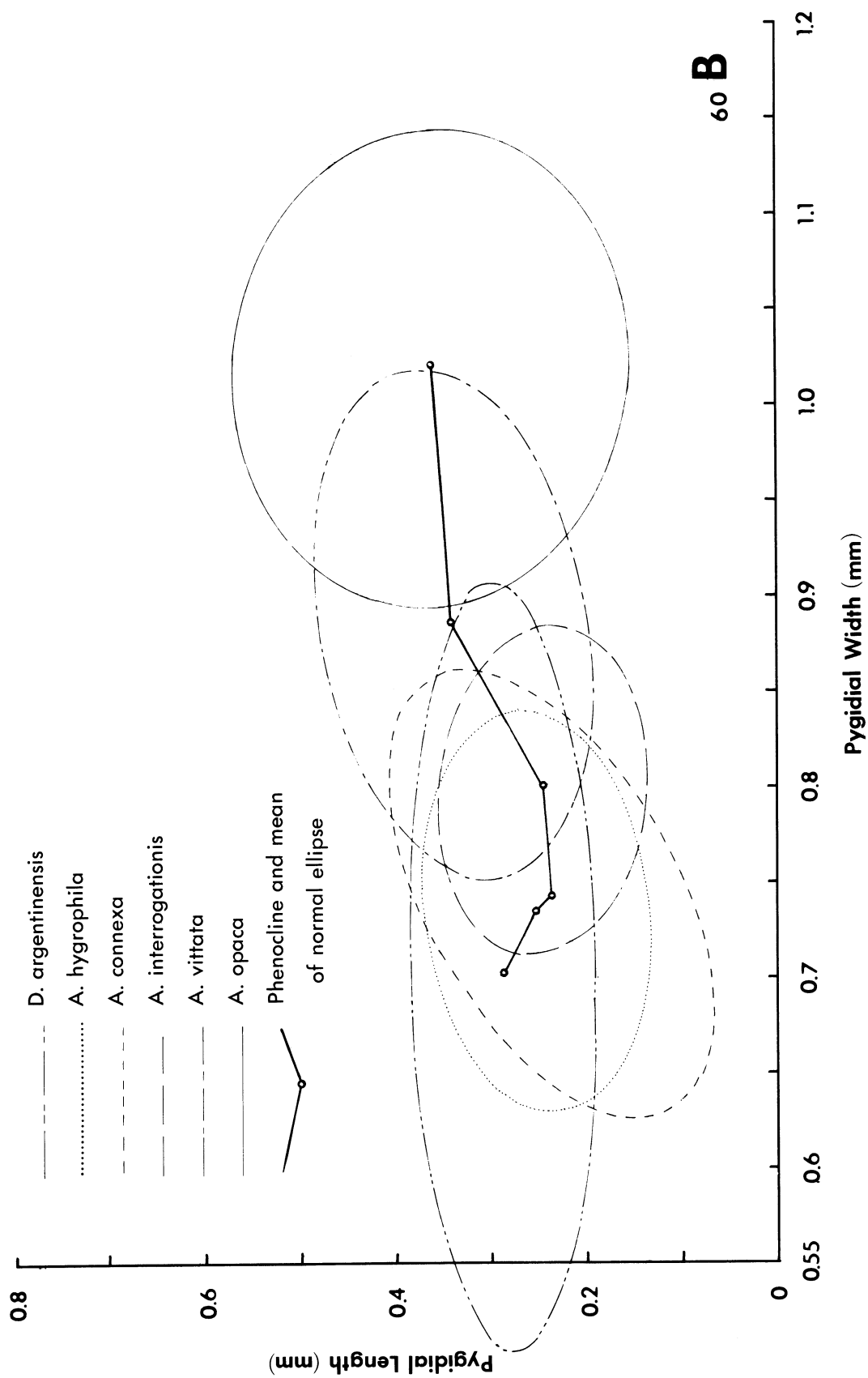


FIGURE 60.—Means and bivariate normal ellipses (first version) for relations in flea beetles between pygidial width and length. A, Females. B, Males. Paraguayan and Amazonian forms of *Agasicles opaca* are combined.

bined fasciate forms, the normal ellipses show no clear taxonomic discrimination among the species of *Agasicles*.

The configuration of the evolutionary trend line is remarkable. It shows a very large decrease in both variates from *Disonycha argentinensis* to *Agasicles hygrophila* and a further marked decrease in the IAW continuing to *A. connexa*. Then there follows an increase in IAW with a decrease in IOW continuing to *A. interrogationis*. Both variates increase moderately, continuing to *A. vittata*, followed by the greatest increase in both variates continuing to the combined fasciate forms.

The striking irregularities in this pair of phenoclines demonstrate the latitude of diversity of widths that can occur in the flea beetles independently of host-plant stem diameters and independently of a general trend of increasing flea beetle body size (compare with figs. 50 and 52). None of these widths abut against the interior of the stem cavity or earthen pupal cell. These widths undergo as much change among the closely related species as among the less related. Despite the irregular phenocline for this character, its usefulness for taxonomic purposes is not borne out by the consistent alinement of the normal ellipses.

Figure 55 represents the relationship of maximum width of the base of the black U-shaped elytral marking (U2W, fig. 46) to minimum width of the base of the ivory U-shaped elytral marking (U1W, fig. 46). The normal ellipses for each of the species show various orientations, with all coefficients of correlation negative except for female *Agasicles connexa* and male *Disonycha argentinensis*. The ellipses for the combined fasciate forms are completely discrete, and those for *A. hygrophila* overlap only slightly those for *A. connexa* and *A. vittata*. This character is diagnostic for the identification of the combined fasciate forms and for *A. hygrophila*.

The phenocline is remarkable for the out-of-line or switchback position of the mean point for *Agasicles vittata*. This discontinuity is also evident on figures 51, 52, 56, and 58 and may point to a more remote relationship with *A. interrogationis*. The increase in U2W is probably related to body elongation in the process of size increase in *Agasicles* species; and in this connection, the mean values for the character proportion are nearly equal for *A. hygrophila* and its closest extrageneric relative, *Disonycha argentinensis*. There is the usual concordance in the trend lines for the females and males, indicating that there is little or no sexual dimorphism shown by this pair of characters.

Figure 56 represents the relationship of antennal length (AL) to metathoracic tibial length (MTL). The normal ellipses are all consistently aligned and have positive coefficients of correlation, with the exception of the female *Disonycha argentinensis* ellipse, which is rotated more than 90° counter-clockwise to a negative coefficient of correlation, in contrast with the ellipse for the male. No clear taxonomic discrimination is evident among these ellipses.

For the first time, the mean point of a vittate *Agasicles*, *A. vittata*, falls closer to *A. opaca* along the phenocline than do two other vittate species, in this case, *A. interrogationis* and *A. connexa*. As shown in table 5, this proximity reappears in the phenoclines for antennal segments (figs. 57, 58, and 60). In all these cases, the greater proximity is limited to the females and is evidence of sexual dimorphism (which is less obvious in figs. 56–58 but very obvious in fig. 60).

The phenocline between *Agasicles hygrophila* and fasciate *A. opaca* is nearly straight, with both variates increasing in value and their mean points being rather evenly distributed along its length. A decrease in length occurs in both the antenna and the tibia between *Disonycha argentinensis* and *A. hygrophila*. Also, these and the next two sets of measured antennal characters are pairs of lengths and cannot show the slenderization that has taken place in the antennae and legs (femora) of *Agasicles* as compared with *Disonycha argentinensis* (figs. 1–6).

Figure 57 represents the relationship of the lengths of the fourth antennal segment (4AL) and the third antennal segment (3AL). The normal ellipses are consistently aligned and have positive coefficients of correlation, with the exception of the female *Disonycha argentinensis* and female *Agasicles connexa* ellipses. The ellipse for females of *A. connexa* is inordinately large because of the small size of the measured sample and its great variation. The normal ellipses show no clear taxonomic discrimination among species along the phenocline.

The phenocline shows the two antennal segments gradually and rather evenly increasing in length from *Agasicles hygrophila* through the combined fasciate forms, with a marked, seemingly spurious deviation by the female of *A. connexa*. From *Disonycha argentinensis* to *A. hygrophila* there is a significant reduction in length of 3AL but only a slight reduction in 4AL.

Figure 58 represents the relationship of the

lengths of the sixth antennal segment (6AL) and the fifth antennal segment (5AL). All the normal ellipses have positive coefficients of correlation. In the females there is no elliptic angle exceeding 45°, while in the males the alinement is more nearly perfect, with elliptic angles not exceeding more than a few degrees. All of the ellipses broadly overlap one another and show no clear taxonomic discrimination among species along the phenoclines.

Along the phenocline this set of relationships shows the greatest proximity between the vittate *Agasicles* species and *A. opaca*. The phenoclines are almost straight, with about a 1 : 1 slope, indicating that antennal segments have increased in size rather regularly in the evolutionary course. As it does in the phenoclines for other plottings, *Agasicles vittata* deviates slightly from the usual trend. *Disonycha argentinensis* makes a similar deviation from the general course of this trend.

Figure 59 represents the relationship of the length of the seventh antennal segment (7AL) and its width (7AW). The normal ellipses for the females show very little alinement, and the axes for *Agasicles connexa* and *A. vittata* have negative coefficients of correlation. In considerable contrast, the ellipses for the males are somewhat consistently alined, and only the one for *A. connexa* has a slight negative coefficient of correlation. There is much overlapping and some near superposition of the ellipses except for that of combined *A. opaca* forms, which is nearly discrete for the females and completely so for the males. In the next section, we will see from the second-version phenoclines that this discreteness of combined *Agasicles opaca* forms is lost to a considerable degree when the samples are subdivided geographically.

The phenocline takes a rather uneven course, but there is clear concordance between the trends for females and males. Between *Disonycha argentinensis* and *Agasicles hygrophila* there is a slight reduction in the width of the antenna, and between *D. argentinensis* and *A. vittata* there is a slight average decrease in the width as the length gradually increases. This trend may also be a manifestation of the slenderization of appendages that facilitate fitting the vittate species of *Agasicles* within the confines of the stem cavity. The steep slope of the phenocline between *A. vittata* and the combined fasciate *A. opaca* forms may reflect a reversal in trend afforded by the lack of restriction inside the large stem cavity of *Alternanthera hassleriana*.

Figure 60 represents the relationship of pygidial

width (PyW) and pygidial length (PyL). The normal ellipses for the females show little alinement, with the ones for *Agasicles connexa* and *A. interrogationis* having negative coefficients of correlation and affording taxonomic discrimination. In considerable contrast, the ellipses for the males are somewhat consistently alined with the ones for *A. interrogationis* and combined *A. opaca* forms and have only slightly negative coefficients of correlation.

A much greater contrast exists between the phenoclines for the females and the males. As pointed out earlier, this is a manifestation of obvious sexual dimorphism and reflects the development of the keellike horns on the female's pygidium, the "key" of the external genitalia characteristic of the genus *Agasicles*. This key is vestigial in the males. But developed on the venter of the male abdomen is the remarkable cavity, or "lock," which receives the key of the external genitalia. Because of lack of suitable corresponding reference points in most females, no measurements were made of the lock in this study.

In the females, between *Disonycha argentinensis* and *Agasicles connexa*, the phenocline shows that the increase in width of the pygidium is accompanied by little change in length. But continuing to *A. interrogationis*, there is a striking increase in length, with little increase in width. A significant reduction in length with a small increase in width ensues to *A. vittata*. A large increase in width, with a small decrease in length, follows to the combined *A. opaca* forms. In comparison, in the males, between *A. hygrophila* and the combined *A. opaca* forms, the width increases with the overall body size, but the length diminishes somewhat before gradually increasing between *A. interrogationis* and the combined fasciate forms. The sexually dimorphic external genitalia seemingly evolved de novo and may have been instrumental in the speciation of *Agasicles*.

Table 5 summarizes the proximity between the vittate *Agasicles* and the combined fasciate *A. opaca* forms, based on phenoclinical distances for each of the 11 character pairs. As already noted, greater proximity does occur between vittate *A. vittata* and fasciate *A. opaca* than between vittate *A. interrogationis* and vittate *A. connexa*. This greater proximity is limited to females for the obvious sexually dimorphic character pair PyW to PyL, and for the three less obvious sexually dimorphic character pairs that involve antennal length, namely, AL to MTL, 4AL to 3AL, and 6AL to 5AL.

Table 5.—First-version phenocline distances between mean points of character pairs of *Agasicles* species as shown in figures 50–60. Decreasing values of differences indicate increasing proximity between the vittate *Agasicles* species and *A. opaca*. Negative values indicate that the distance between vittate *A. vittata* and fasciate *A. opaca* is less than the distance between vittate *A. interrogationis* and vittate *A. connexa*

[Millimeters]

Character pair (x to y)	Females			Males		
	<i>A. vittata</i> to <i>A. opaca</i>	<i>A. connexa</i> to <i>A. interrogationis</i>	Difference	<i>A. vittata</i> to <i>A. opaca</i>	<i>A. connexa</i> to <i>A. interrogationis</i>	Difference
PrW to PrL (fig. 50)	152	13	+139	152	6	+146
EL to EW (fig. 51)	90	27	+63	84	38	+46
BL to BTh (fig. 52)	75	30	+45	70	20	+50
HW to HL (fig. 53)	62	15	+47	61	6	+55
IOW to IAW (fig. 54)	107	29	+78	112	22	+90
U2W to U1W (fig. 55)	125	34	+91	117	26	+91
AL to MTL (fig. 56)	26	38	-12	58	34	+24
4AL to 3AL (fig. 57)	34	43	-9	61	34	+27
6AL to 5AL (fig. 58)	45	70	-25	64	52	+12
7AL to 7AW (fig. 59)	97	22	+75	106	19	+87
PyW to PyL (fig. 60)	70	91	-21	68	28	+40
Total	883	412	+538 -67	953	285	+668 -0

The straight-line distances between the mean points of character pairs for *Disonycha argentinensis* (base zero) and those for each *Agasicles* species are given in table 6. The progression from *D. argentinensis* to *A. opaca* for each of the mean points varies from the more even (♀ U2W to UIW and ♂ PyW to PyL) to the more uneven (♀ IOW to IAW and ♂ IOW to IAW). The totals for each of the flea beetle species constitute a rather even progression for both females and males, with *Agasicles vittata* showing a tendency to deviate. For those phenoclines that are irregular, the serial order presented in the dendrogram (fig. 40) and in the charts results in greatest consistency. Different ordering of the series results in greater overall inconsistency. For these reasons, and in consideration of the background information previously given, we believe the relative proximity of the mean points for the *Agasicles* species and *Disonycha argentinensis* expresses relationship.

We also note from table 6 that for only a single character pair, IOW to IAW, does a female vittate *Agasicles* exceed *A. opaca* in the distance separating it from *Disonycha argentinensis*. In the males, *A. opaca* is not exceeded on a straight line in any of the 11 character pairs. Additionally, 7 of the 11 female maximum distances correspond to those of the males, while 9 of the 11 minimum

distances (not indicated in table 6) correspond to those of the males.

Flea beetles (subspecific forms of *Agasicles opaca*)

The quantitative studies reported in the previous section relate to flea beetle species or populations that we consider as being reproductively isolated. Figures 1–6 show differences in the external lock-and-key genitalia of these forms, while figures 26–31 show less obvious differences in the uncleared aedeagi. Additional study material acquired in South America in 1975 enables us to reconsider the subspecific forms of *Agasicles opaca* in more detail.

Previously, when our material was limited to the two extreme ends of their range, we considered that the fasciate *Agasicles* might be composed simply of two species. This judgment was based on markings and on a rather wide separation between most of the mean points of the two forms along the phenocline in which the lower Amazonian form is consistently most distantly removed from *Disonycha argentinensis* (in table 6, we show only the straight-line distance for the combined Paraguayan and Amazonian forms of *Agasicles opaca*). Furthermore, we anticipated that the two forms would separate as Paraguayan and Amazonian. However, additional samples have tended to obscure the separation

Table 6.—Straight-line distances between mean points (figs. 50–60) of body proportions of *Disonycha argentinensis* and *Agasicles* species. Maximums within vittate *Agasicles* species are in brackets. Maximums that are concordant between females and males are starred

Character pair (x to y)	[Percent of total]					
	<i>D.</i> <i>argentinensis</i>	<i>A.</i> <i>hygrophila</i>	<i>A.</i> <i>connexa</i>	<i>A.</i> <i>interrogationis</i>	<i>A.</i> <i>vittata</i>	<i>A.</i> <i>opaca</i>
FEMALES						
PrW to PrL (fig. 50)	0	[19.5]*	17.6	17.6	16.2	29.2
EL to EW (fig. 51)	0	7.0	5.1	[17.8]*	15.4	54.7
BL to BTh (fig. 52)	0	0.9	9.0	[21.4]	18.3	50.4
HW to HL (fig. 53)	0	[22.4]*	8.0	20.0	16.0	33.6
IOW to IAW (fig. 54)	0	18.7	[24.6]*	23.4	18.7	14.6
U2W to U1W (fig. 55)	0	0.6	17.6	[24.8]*	17.6	39.4
AL to MTL (fig. 56)	0	6.0	6.0	22.1	[26.8]*	37.9
4AL to 3AL (fig. 57)	0	13.6	7.8	20.5	[23.0]*	35.0
6AL to 5AL (fig. 58)	0	6.0	10.3	[26.8]	23.1	33.9
7AL to 7AW (fig. 59)	0	6.5	13.6	[18.8]	17.2	43.9
PyW to PyL (fig. 60)	0	3.0	10.1	[26.8]	23.3	37.0
Total	0	9.0	13.0	22.3	19.6	36.2
MALES						
PrW to PrL (fig. 50)	0	[19.7]*	15.3	16.4	16.2	32.4
EL to EW (fig. 51)	0	5.6	2.3	[18.5]*	18.1	55.6
BL to BTh (fig. 52)	0	2.8	2.5	15.9	[16.5]	61.1
HW to HL (fig. 53)	0	[19.4]*	5.1	11.2	11.2	53.1
IOW to IAW (fig. 54)	0	16.1	[22.6]*	21.6	15.8	24.0
U2W to U1W (fig. 55)	0	2.8	17.5	[23.2]*	17.3	39.1
AL to MTL (fig. 56)	0	6.5	6.9	17.8	[23.1]*	45.8
4AL to 3AL (fig. 57)	0	12.9	10.4	15.4	[20.4]*	41.0
6AL to 5AL (fig. 58)	0	3.1	9.6	23.1	[23.8]	40.4
7AL to 7AW (fig. 59)	0	4.9	12.9	14.7	[20.0]	47.6
PyW to PyL (fig. 60)	0	5.4	7.1	14.3	[26.8]	46.5
Total	0	8.7	11.5	18.1	19.3	41.9

along the phenocline and have revealed no clear evidence of reproductive isolation. Besides, instead of a Paraguayan and an Amazonian form, we now consider three subspecific forms as more likely.

Accordingly, we assigned the samples of *Agasicles opaca* to three very large geographic regions among which, we postulate, there is now only restricted gene flow. The first of these regions is the broad deltaic plain of the lower Amazon River. Much of this is open landscape studded with isolated insolated lagoons that are natural habitats of *Alternanthera hassleriana*, the normal host of *Agasicles opaca*. A broad region of forest and a long stretch of rapids of the Madeira River together with a narrow alluvial plain and a paucity of lagoons separate the lower Amazon from the second region, the Plains (Llanos) of Mojós. Within the Amazon Basin, this vast region of seasonal flooding and open

landscapes constitutes a major center of *Alternanthera hassleriana* and *Agasicles opaca*. Within 600 kilometers of the Plains of Mojós are the lagoons and associated wetlands of the Paraguay River basin, the third major center of *Agasicles opaca* and its host plant. This vast region includes the Pantanal and much of the Gran Chaco. The interface of the Madeira River (Amazon) basin and the Paraguay River basin crosses the Santa Cruz Department of Bolivia and the Planalto do Mato Grosso. The first is a region of mostly low but seasonally dry relief, and the second is a region of narrow valleys. Both seem to lack conditions needed for lagoon formation. Under present conditions, a trickle of gene flow could exist between the Candelaria River (Paraguay Basin) and the upper reaches of the Guaporé River (Amazon Basin).

The ecological homology existing among the

species of *Agasicles*, together with their biogeography and the dispersal capability demonstrated in the United States by *Agasicles hygrophila*, indicate that gene flow may be important as a cohesive force in the speciation within this genus (Mayr 1970). However, Ehrlich and Raven (1969) and Ehrlich et al. (1975) consider that "gene flow in nature is much more restricted than is commonly thought and experimental evidence is badly needed to document the extent to which it does occur." They believe that natural selection operating upon localized small populations is the more important evolutionary mechanism. They consider further that climatic difference constitutes an important selective feature: "Our data support the generalization that differentiation will occur in the presence of gene flow or will not occur in its absence depending on the regime."

The results we present next in this and in the following section will show that divergence among the three geographic forms of *Agasicles opaca* is less than has occurred among the four vittate *Agasicles* species. However, the divergences between the vittate group of species and the fasciate group of forms are mostly even more extensive. We interpret these findings to mean that having undergone most of its evolution interacting with small-stemmed alligatorweed, fasciate polytypic *Agasicles opaca* diverged from the vittate forms, continuing its evolution interacting mostly with the oversized stems of *Alternanthera hassleriana*. While this release from interaction with small stems relates to an accelerated rate of divergence from the vittate forms, it also relates to slowed evolution of reproductive isolation and therefore speciation among the fasciate forms. Furthermore, the larger-sized fasciate *Agasicles* forms may have greater vagility than the vittate species, which remain under the constraints of restrictive undersized host-plant stems. Greater vagility should result in greater gene flow over geographic barriers, which we judge to be comparable in resistance against either the vittate or the fasciate *Agasicles* forms. We conclude that the slowed speciation rate among the fasciate *Agasicles* forms may be a result of greater gene flow.

However, there seems to be little in our field results to support this conclusion. Probably because of the floating nature and other attributes of its host plant, *Alternanthera hassleriana* (fig. 7), the fasciate *Agasicles* forms (and *Vogtia malloi*) are not as extirpative in their depredations as are the vittate *Agasicles* species (and *Vogtia malloi*) on alligatorweed. As a result *Alternanthera hassleriana* occurs

more generally and evenly over the aquatic portions of its habitat than does alligatorweed. The reverse is true, however, for their occurrences over the terrestrial portions of their habitat ranges (Vogt et al., cited in footnote 8). To match this information indicating greater homeostasis in the interaction of host plant and fasciate *Agasicles* species as compared with the interaction of host plant and vittate *Agasicles* species, we have no information on the dispersal capability of the fasciate *Agasicles* forms to compare with what we have on *A. hygrophila* in the United States (Vogt et al., cited in footnote 20).

With these considerations in mind, we proceed with an analysis of the second-version phenoclines and the normal ellipses for the fasciate *Agasicles* forms.

The most variable character within *Agasicles opaca* is the elytral markings. In figure 61, 10 graded variants of elytral markings represent the range of variation in 137 specimens of *A. opaca* from the 3 regions just described. Since we will consider quantitatively only one set of character proportions based on markings, namely U2W to U1W, we present in table 7 the frequency distribution for the 10 illustrated variants. It is evident that the lower Amazon River form and the Paraguay River form rather clearly constitute two rather even, distinct patterns, while the distribution of the Plains (Llanos) of Mojós form tends to make a rather uneven overlapping third distribution pattern.

We now consider the three geographic forms of *Agasicles opaca* quantitatively with respect to the same 11 pairs of character pairs studied in the previous section. Figures 62 through 72 show the bivariate normal ellipses for the 11 different character proportions. As before, each set is composed of a series for the females (A) and a series for the males (B). In each series the heavy line connecting the mean points for each subspecific form is the phenocline. It is continuous with the phenocline of the vittate species, which is shown without normal ellipses. A dotted line connects the phenoclines of the vittate species and the fasciate forms, and, at the other end, the mean point for *Disonychia argentinensis*. The total phenocline constitutes the second version of the *Disonychia-Agasicles* phenocline. Again the sequence of the four vittate species and the three fasciate subspecific forms is the same as that given for Recent time in the dendrogram shown in figure 40. The scales of the second-version phenoclines are adjusted to be subequal to those of the first version.

Generally, for most character proportions, the

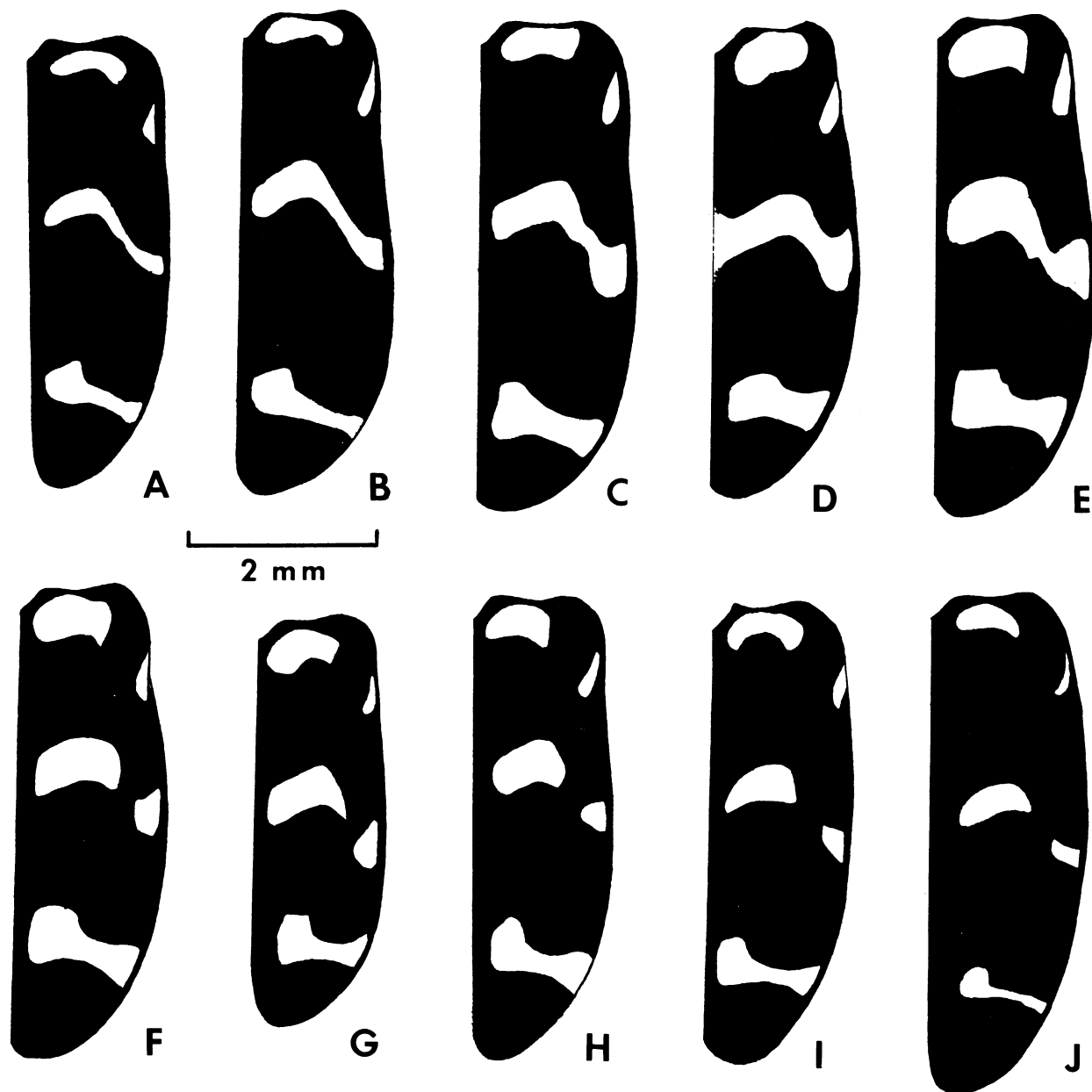


FIGURE 61.—Ten graded variants of elytral markings, A to J, selected from the 137 specimens (70 females and 67 males) of *Agasicles opaca* studied quantitatively (described in table A-9). Variant J is intermediate between variants I and A. Similarly each of the other variants is intermediate between the preceding and succeeding variant.

phenoclines of the fasciate forms of *Agasicles* are shorter than those for the vittate species and undergo somewhat comparable changes. Usually, the concordance between the female and male phenoclines more or less continues. As compared with the first-version phenoclines presented in the previous section, we find less separation between the mean points of the proximate forms of vittate and fasciate *Agasicles* for most character pairs. This change is tabulated under “reduction (–) or in-

crease (+) of difference” in table 8. In a few character pairs, the reduction is marked. This increased proximity results from organizing the samples of *Agasicles opaca* into three geographical forms, of which individuals of the Paraguay River form are significantly smaller in size than those of the lower Amazon River form. While the proximity between vittate *Agasicles vittata* and the Paraguay River form of fasciate *A. opaca* increases along the phenocline, there is no increase in the number of

Table 7.—Frequency distribution, in percentage of representation, of the 10 variants of elytral markings of *Agasicles opaca* illustrated in figure 61. Percentages are based on clusterings of the 137 specimens described in table A-9

Geographic area	Variant illustrated in figure 61									
	A	B	C	D	E	F	G	H	I	J
Lower Amazon River (<i>n</i> =33)	0	12.1	45.5	36.4	3.0	0	3.0	0	0	0
Plains (Llanos) of Mojós (<i>n</i> =30)	6.7	6.7	0	10.0	3.3	0	13.3	6.7	43.4	10.0
Paraguay River (<i>n</i> =74)	0	0	0	2.7	19.0	25.7	39.2	9.5	4.1	0

Table 8.—Second-version phenocline distances between mean points of character pairs of *Agasicles* species as shown in figures 62-72. Decreasing values of differences indicate increasing proximity between the vittate *Agasicles* species and the Paraguay River form of *A. opaca*. Negative values indicate that the distance between vittate *A. vittata* and the Paraguay River form of fasciate *A. opaca* is less than the distance between vittate *A. connexa* and *A. interrogans*. The reduction or increase of difference is with reference to the female and male differences given in table 5

Character pair (<i>x</i> to <i>y</i>)	Females										Males			
	[Millimeters]													
	<i>A. vittata</i> to Paraguay River form of <i>A. opaca</i>	<i>A. connexa</i> to <i>A. interrogans</i>	Dif- ference	Reduction (-) or increase (+) of difference	<i>A. vittata</i> to Paraguay River form of <i>A. opaca</i>	<i>A. connexa</i> to <i>A. interrogans</i>	Dif- ference	Reduction (-) or increase (+) of difference	<i>A. vittata</i> to Paraguay River form of <i>A. opaca</i>	<i>A. connexa</i> to <i>A. interrogans</i>	Dif- ference	Reduction (-) or increase (+) of difference	<i>A. vittata</i> to Paraguay River form of <i>A. opaca</i>	<i>A. connexa</i> to <i>A. interrogans</i>
PrW to PrL (fig. 62)	139	13	+126	-14	136	10	+126	-20						
EL to EW (fig. 63)	65	26	+40	-23	55	32	+24	-22						
BL to BTh (fig. 64)	44	31	+13	-32	48	21	+28	-22						
HW to HL (fig. 65)	53	16	+37	-10	53	8	+45	-10						
IOW to IAW (fig. 66)	98	27	+86	+8	95	21	+93	+3						
U2W to U1W (fig. 67)	139	35	+104	+13	122	33	+89	-3						
AL to MTL (fig. 68)	19	39	-20	-8	27	32	-5	-30						
4AL to 3AL (fig. 69)	19	46	-37	-28	33	38	-6	-33						
6AL to 5AL (fig. 70)	20	66	-47	-22	23	49	-27	-39						
7AL to 7AW (fig. 71)	69	21	+48	-27	74	18	+56	-31						
PyW to PyL (fig. 72)	58	83	-27	-6	36	27	+13	-27						
Total	723	403	+454	+21	702	289	+474	+3						
			-131	-170			-38	-237						

character pairs having vittate *Agasicles* mean points nearer those of the fasciate forms than those of other vittate species.

In part, because of this increased proximity along the phenocline, there is greater overlapping of the ellipses of the fasciate and vittate *Agasicles* species. Also, in part, because there is too little separation along the phenocline, there is no significant taxonomic discrimination among the normal ellipses of the three forms of fasciate *Agasicles opaca*. For most character pairs, the normal ellipses of the fasciate forms have comparable form and are oriented similarly to those of the vittate species. Generally, for each character pair, one of the three separate normal ellipses of *A. opaca* or more extends beyond the corresponding normal ellipses for the 1960–61 combined samples presented in the previous section (figs. 50–60). Three causes for these differences are: (1) reduction of sample size through division into three geographic forms; (2) increase of variance as a result of additions to samples from the collections in 1975; and (3) inadequate adjustment of the x and y scales to compensate for calibration errors (see p. 43) applied exclusively in the previous section to the 1960–61 samples.

Figure 62 represents the relationship of pronotal width (PrW) to pronotal length (PrL). The ellipses show the same strong positive intercharacter correlation as do those of the vittate species shown on figure 50. In both sexes the phenocline changes slope to show an extended strong tendency for elongation of the prothorax with little increase in width. This change is inconsistent with the concept that release from interaction with a constrictive stem should result in more broadening than elongation. Possibly, the effects of the release have run their course, and another adaptive course has set in. Although the phenocline is moderately long (longer than that of the vittates in the males), the ellipses overlap very broadly, there being no significant taxonomic discrimination. The ellipses of the individual geographic forms extend beyond those based on the combined 1960–61 samples (fig. 50). In the females, the extension is broad, while in the males, it is narrow.

Figure 63 represents the relationship of elytral length (EL) to elytral, or body, width (EW). Again the normal ellipses show the same strongly positive intercharacter correlation as do the vittate flea beetles (fig. 51). There is no taxonomic discrimination. The ellipses for the females extend beyond those based on the 1960–61 combined samples. Those for the males coincide almost perfectly, fall-

ing slightly within. There is no calibration correction to affect either of these sets of character pairs. The phenoclines for both sexes show a switchback that seems to be comparable to those occurring between vittate *Agasicles interrogationis* and *A. vittata*. Again, as size increases, length increases more than width. However, the general slope of the phenocline changes little in passing from the vittate species through the fasciate forms.

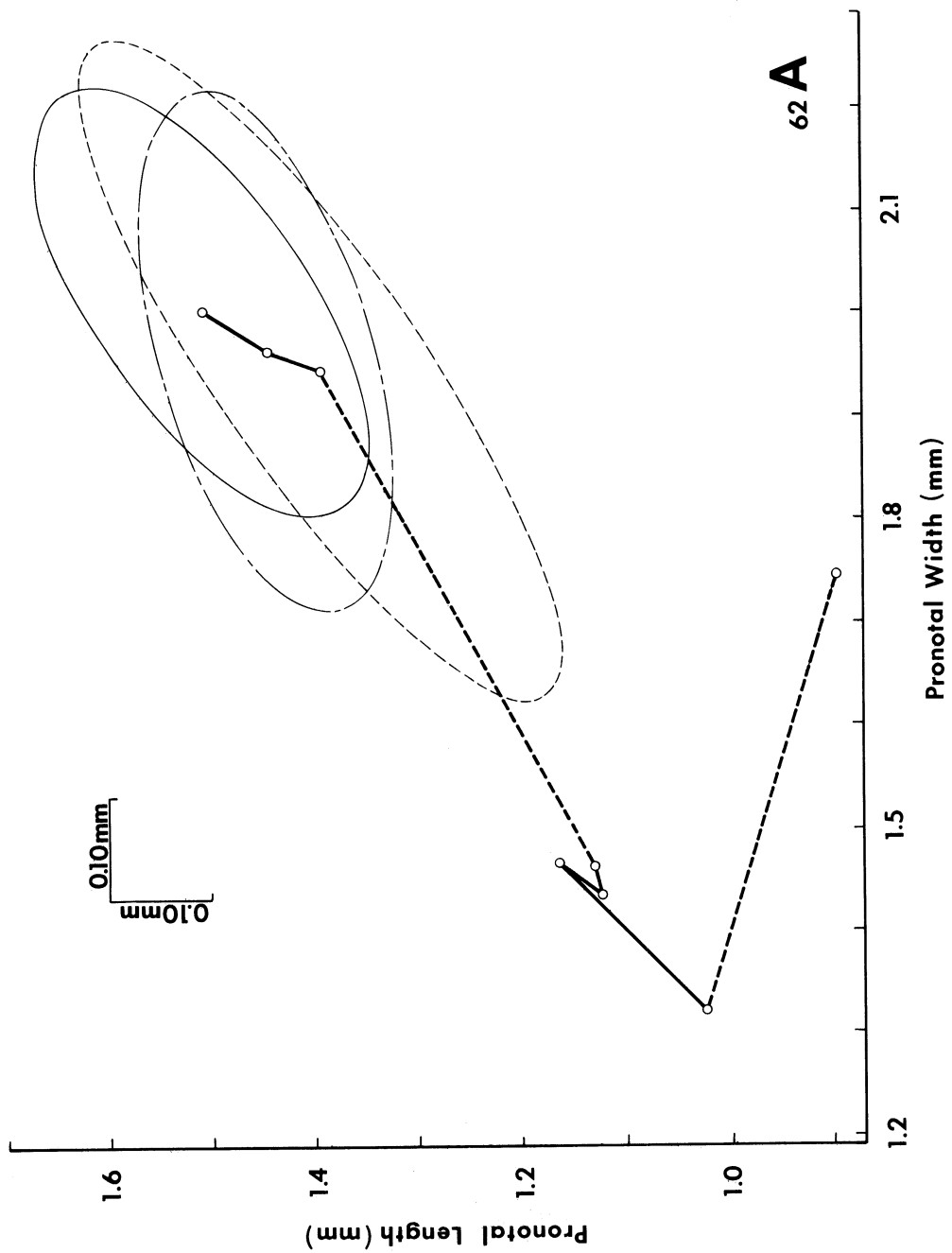
Figure 64 represents the relationship of body length (TBL) to body thickness (BTh). Still again, the ellipses show the same strongly positive intercharacter correlation as do those for the vittate flea beetles (fig. 52). There is wide overlapping and no taxonomic discrimination among the three fasciate forms. The ellipses for the females extend slightly beyond that based on the 1960–61 combined samples. Again, there is nearly perfect coincidence of the ellipses of both sets for the males. As in the previous character proportion, the slope of the phenocline shows no persistent change, and again there is a short switchback that is comparable to that occurring between vittate *Agasicles interrogationis* and *A. vittata*.

This and the two preceding character pairs, the phenoclines of the fasciates, show the late stages of the dramatic size increase that occurred since the vittate ancestral form near *Agasicles hygrophila* first became associated with the floating inflated-stem *Alternanthera hassleriana*. It is clear from the phenoclines that the lower Amazon form is a larger insect than is the Paraguay River form, while the Plains of Mojós form is only slightly larger.

Figure 65 represents the relationship of head width (HW) to head length (HL). These ellipses are closely clustered and are broad to almost circular in form. In these respects, they are similar to those for the vittate flea beetles (fig. 53). The latter ellipses are more variously oriented, however. The ellipses for both sexes of the three forms of *Agasicles opaca* extend widely beyond those based on the 1960–61 combined samples (fig. 53). The scales of the second-version phenoclines are about subequal to those of the first version. The fasciate *Agasicles* species show some of the general directional change that characterizes the vittates.

Figure 66 represents the relationship of interocular width (IOW) to interantennal width (IAW). The normal ellipses tend to show the same positive intercharacter orientation as those for the vittate flea beetles (fig. 54). Although the phenocline is moderately long for the fasciate forms, the ellipses are too

(Continued on page 87.)



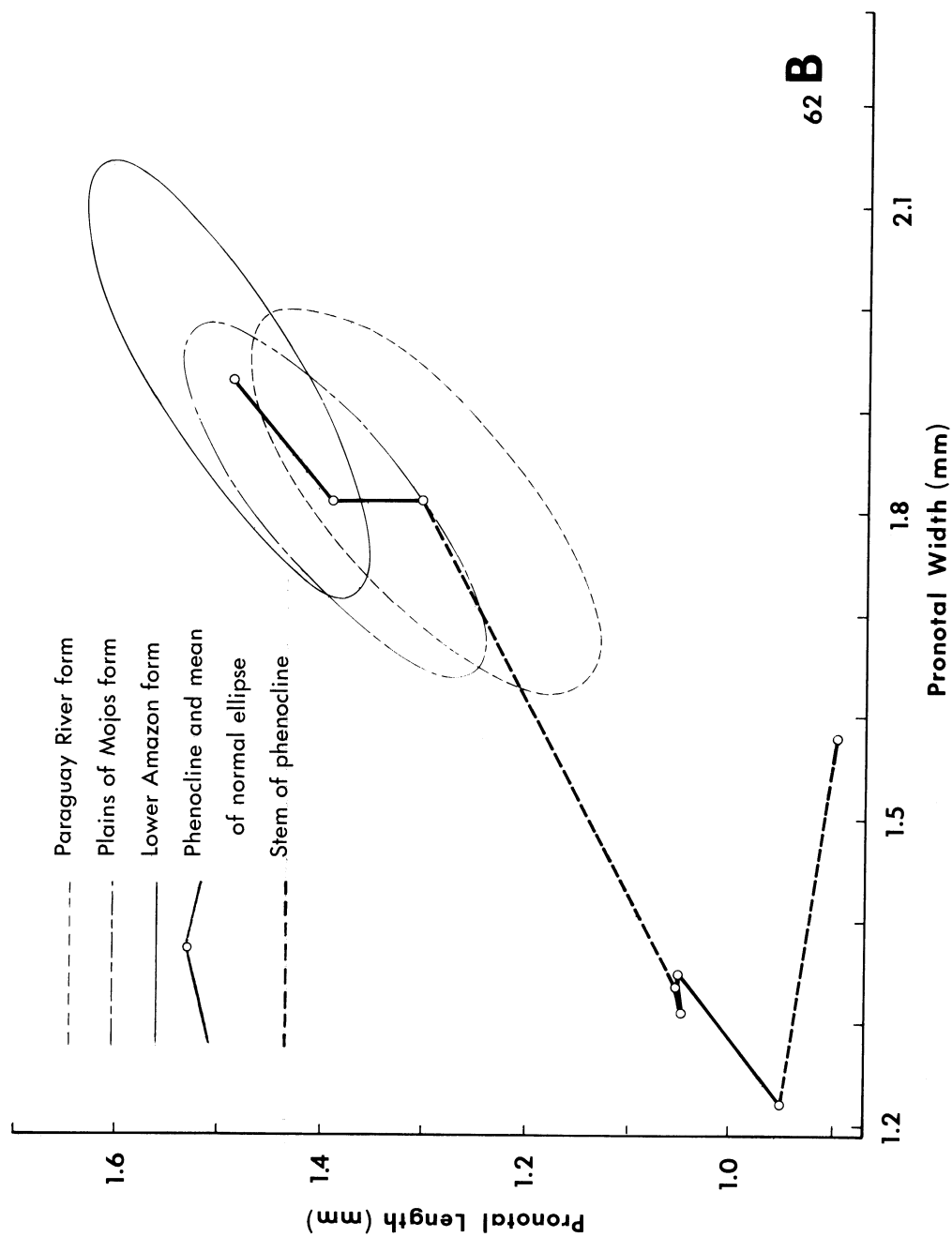


FIGURE 62.—Means and bivariate normal ellipses (second version) for relations in flea beetles between pronotal width and length. A, Females. B, Males. The solid line connecting the mean points for each subspecific form is the phenocline of the fasciate forms. It is continuous with the phenocline of the vittate species, which is shown without normal ellipses. A dashed line connects these two phenoclines and, at one end, the mean point of *Disonycha argentinensis* to form the second-version phenocline.

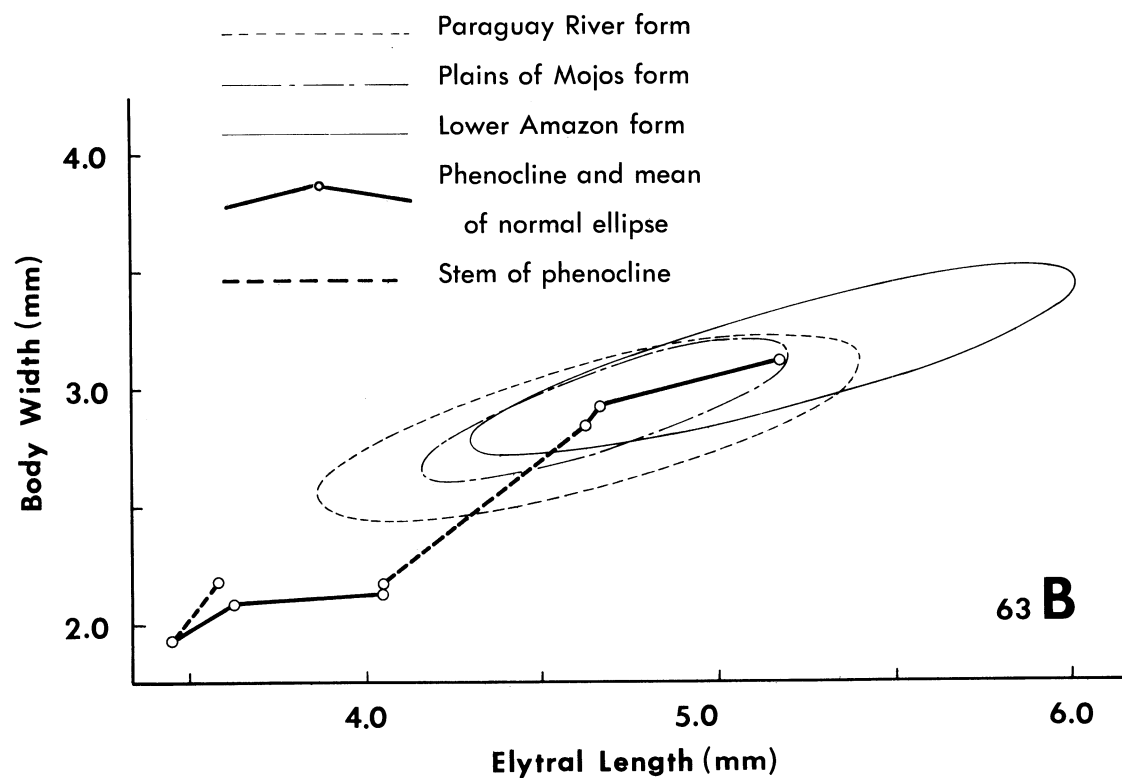
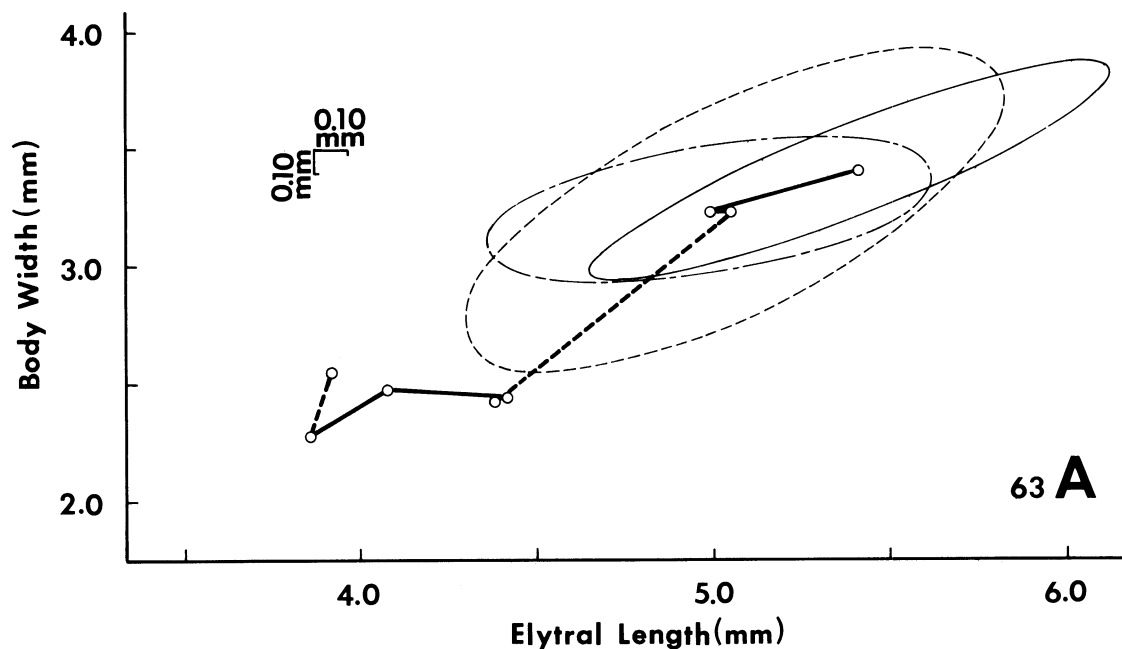


FIGURE 63.—Means and bivariate normal ellipses (second version) for relations in flea beetles between elytral length and width. A, Females. B, Males. The solid line connecting the mean points for each subspecific form is the phenocline of the fasciate forms. It is continuous with the phenocline of the vittate species, which is shown without normal ellipses. A dashed line connects these two phenoclines and, at one end, the mean point of *Disonycha argentinensis* to form the second-version phenocline.

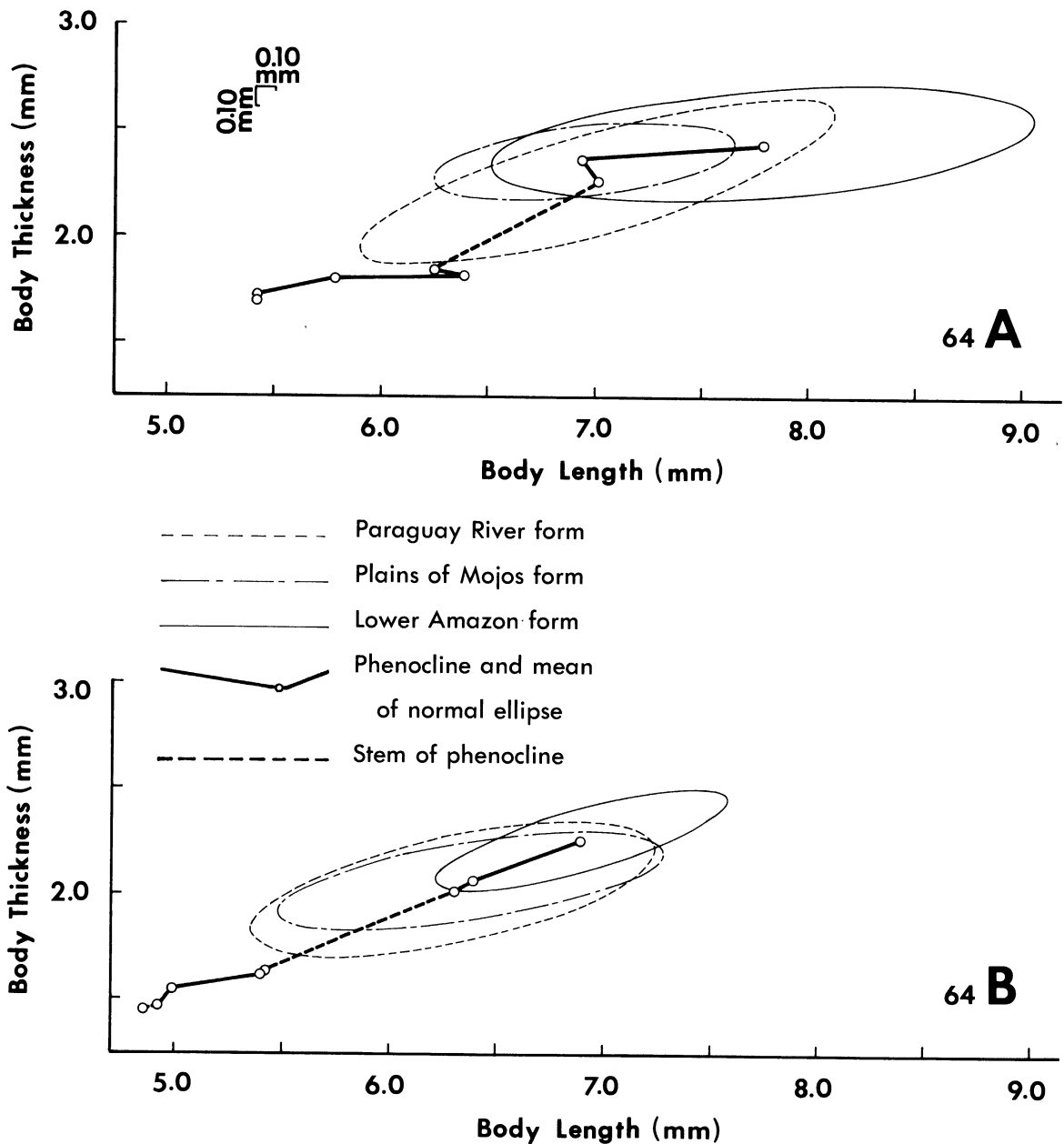


FIGURE 64.—Means and bivariate normal ellipses (second version) for relations in flea beetles between total body length and thickness. A, Females. B, Males. The solid line connecting the mean points for each subspecific form is the phenocline of the fasciate forms. It is continuous with the phenocline of the vittate species, which is shown without normal ellipses. A dashed line connects these two phenoclines and, at one end, the mean point of *Disonycha argentiniensis* to form the second-version phenocline.

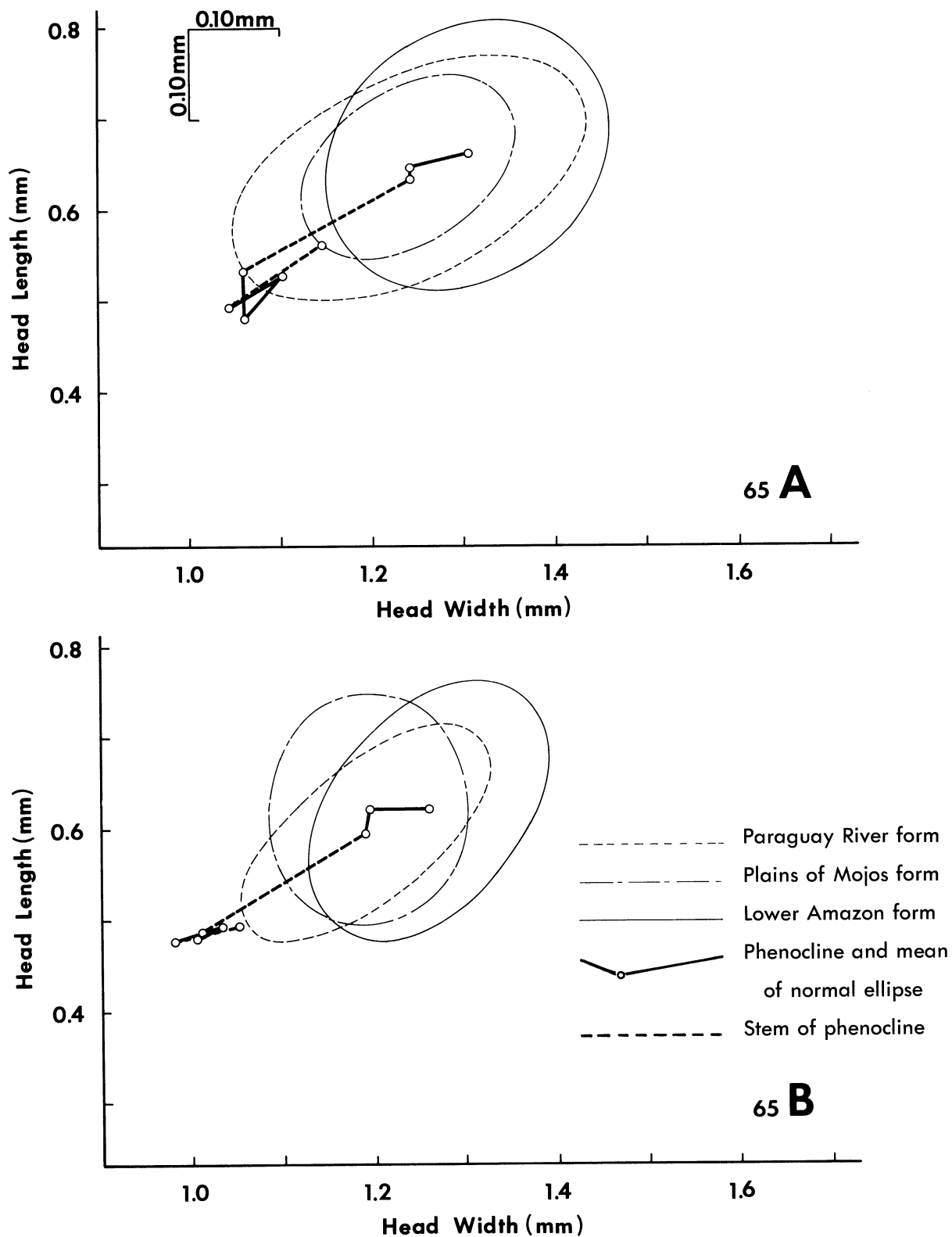


FIGURE 65.—Means and bivariate normal ellipses (second version) for relations in flea beetles between head width and length. A, Females. B, Males. The solid line connecting the mean points for each subspecific form is the phenocline of the fasciate forms. It is continuous with the phenocline of the vittate species, which is shown without normal ellipses. A dashed line connects these two phenoclines and, at one end, the mean point of *Disonychia argentinensis* to form the second-version phenocline.

large and too closely clustered to allow taxonomic discrimination. Although the second-version phenoclines are subequal to slightly smaller than those of the first, the ellipses for both sexes extend widely beyond those based on the 1960–61 combined samples (fig. 54).

Figure 67 represents the relationship of maximum width of the base of the black U-shaped elytral marking (U2W, fig. 46) to minimum width of the base of the ivory-colored U-shaped elytral marking (U1W, fig. 46). As with the vittate species of *Agasicles* (fig. 55), the ellipses for the fasciate forms of *A. opaca* show various orientations that are negative for females of the Plains (Llanos) of Mojós form and for males of the Paraguay River and lower Amazon River forms. But the size and breadth of the ellipses and the moderate phenoclinical distances prevent taxonomic discrimination among the fasciate *Agasicles* for this character pair. The ellipses for both sexes correspond well in general form to the pair based on the 1960–61 combined samples. But for both sexes, the ellipses of the subdivided samples extend moderately beyond those based on the combined samples. The scale for the second-version phenoclines is inadequately adjusted, being somewhat oversized.

We note that the rather long phenocline of the fasciate *Agasicles* shows the same kind of discontinuity, represented by a switchback, that occurs between *A. connexa* and *A. vittata* of the vittate species. This feature is very apparent in the females between the Paraguay River and lower Amazon River forms of the fasciate *Agasicles*. This type of occurrence on the same phenocline between geographically contiguous forms raises some question about the validity of relating such a discontinuity to a major biogeographical isolation, as we have indicated in the case of *A. interrogationis* and *A. vittata* (p. 74). In the same relative positions, this type of discontinuity recurs in both fasciata and vittates in two previous sets of phenoclines (EL to EW and TBL to BTh).

Figure 68 represents the relationship of antennal length (AL) to metathoracic tibial length (MTL). The ellipses show the same strong positive inter-character correlation as do the vittate flea beetles (fig. 56). The ellipses are almost superimposed in the females, for which the phenocline is very short. They overlap broadly in the males, for which the phenocline is quite long. The ellipses for both sexes extend very little beyond the pair based on the 1960–61 combined samples (fig. 56).

The contrast between female and male phenocline

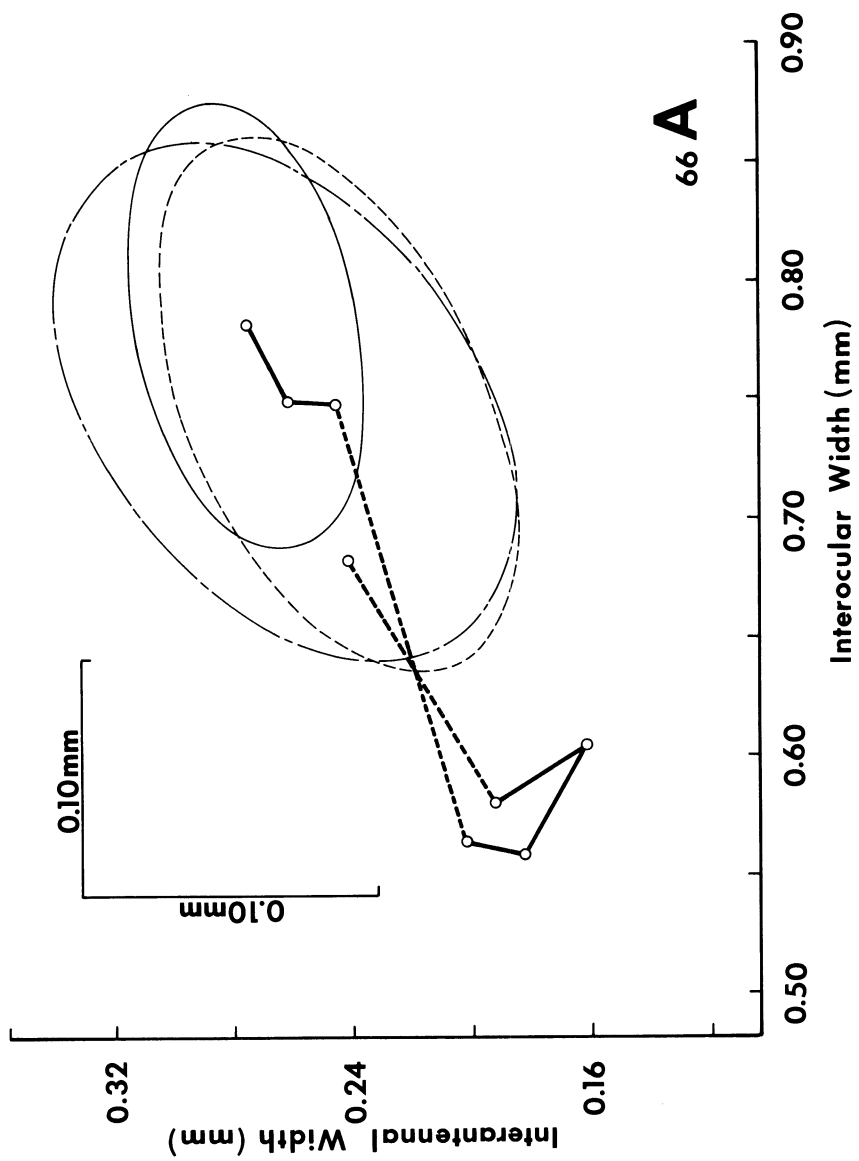
lengths just described is a manifestation of less obvious sexual dimorphism and recurs in the length of antennal character pairs presented in figures 69 (4AL to 3AL) and 70 (6AL to 5AL). As indicated by negative differences in table 8, both female and male phenoclines show greater proximity between the fasciate and vittate *Agasicles* species. In the phenoclines based on the combined forms of fasciate *A. opaca*, the greater proximity is limited to the females (table 5).

Figure 69 represents the relationship of the lengths of the fourth antennal segment (4AL) and the third antennal segment (3AL). The normal ellipses tend to be consistent in form and alignment with those representing the vittate species (fig. 57). There is near superposition for the females and broad overlapping for the males. Having some out-of-line orientation and a broader phenoclinical separation, the male ellipses show some tendency for taxonomic discrimination. Both female and male ellipses extend broadly beyond the pair based on the 1960–61 combined samples (fig. 57). The phenocline is irregularly longer in the females and subequal in the males as compared with those of figure 57 in the previous section.

Figure 70 represents the relationship of the lengths of the sixth antennal segment (6AL) and the fifth antennal segment (5AL). The ellipses show about the same strong intercharacter correlation as do the vittate flea beetles shown in figure 58. Although the phenoclines of the fasciate species are moderately long, especially in the males, the ellipses overlap very broadly and show no taxonomic discrimination except that longer antennal segments characterize the Amazon River form in less than half of the individuals in the females and more than half in the males. The ellipses for both sexes of the three forms of *Agasicles opaca* extend only slightly beyond those based on the 1960–61 combined samples (fig. 58). The phenoclines are slightly longer in both sexes as compared with those of figure 58 of the previous section.

Figure 71 represents the relationship of length of the seventh antennal segment (7AL) and its width (7AW). For females, the normal ellipses are aligned quite closely. This is in contrast with the various elliptic orientations of the female vittate species (fig. 59A). For the males the three ellipses are variously oriented, in contrast with the more consistently aligned male vittate species (fig. 59B). The phenoclines are rather long, and the ellipses are broadly overlapped to nearly superimposed. Al-

(Continued on page 100.)



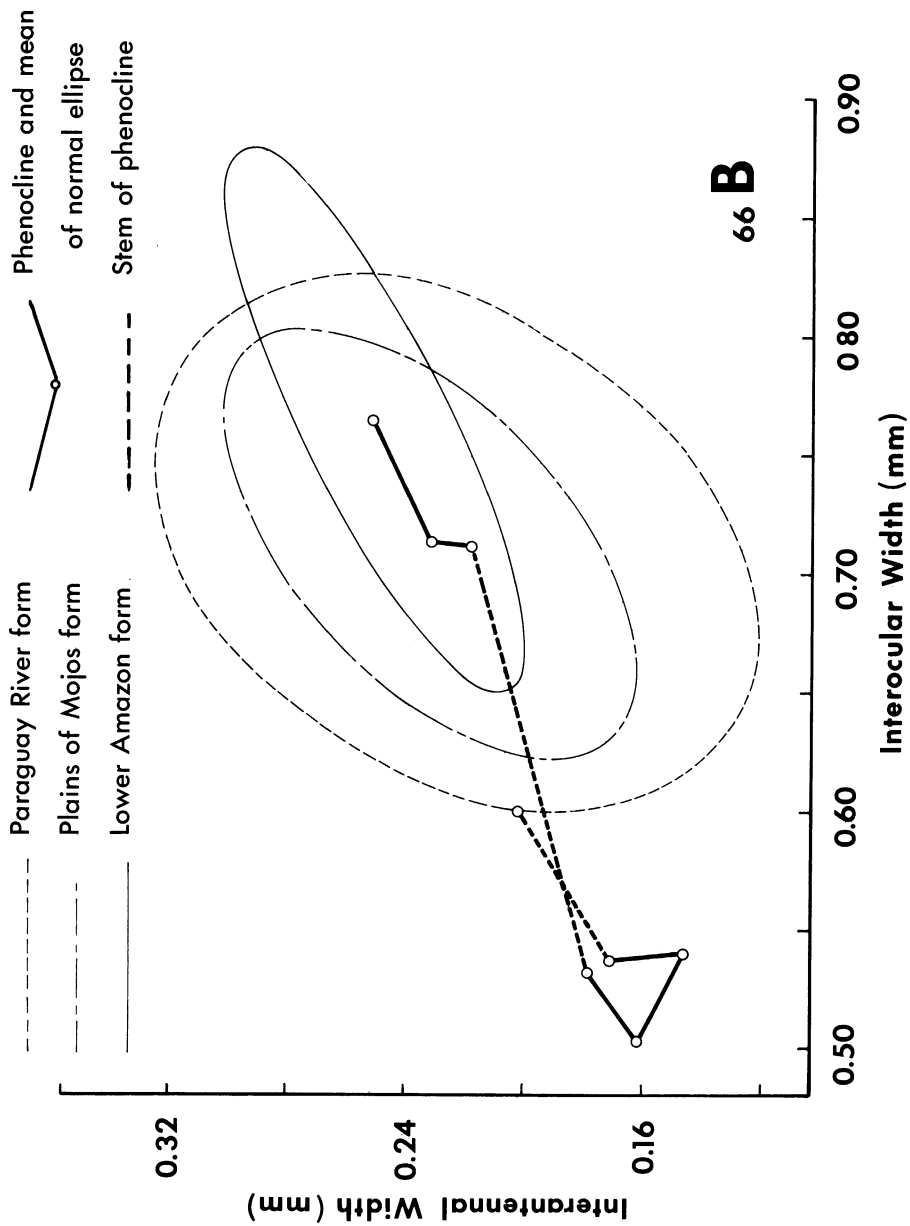
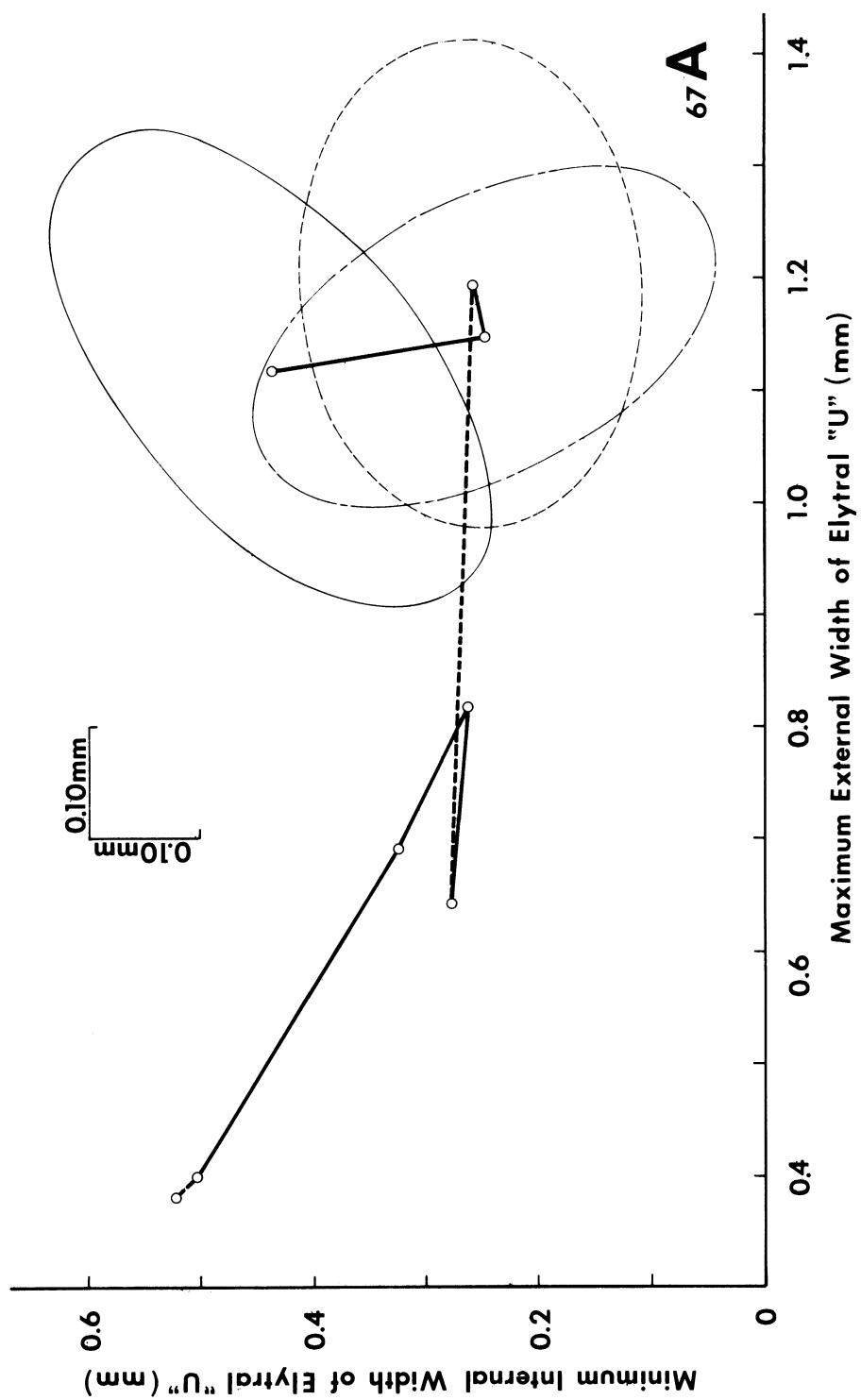


FIGURE 66.—Means and bivariate normal ellipses (second version) for relations in flea beetles between interocular width and interantennal width. A, Females. B, Males. The solid line connecting the mean points for each subspecific form is the phenocline of the fasciate forms. It is continuous with the phenocline of the vittate species, which is shown without normal ellipses. A dashed line connects these two phenoclines and, at one end, the mean points of *Disonycha argentinensis* to form the second-version phenocline.



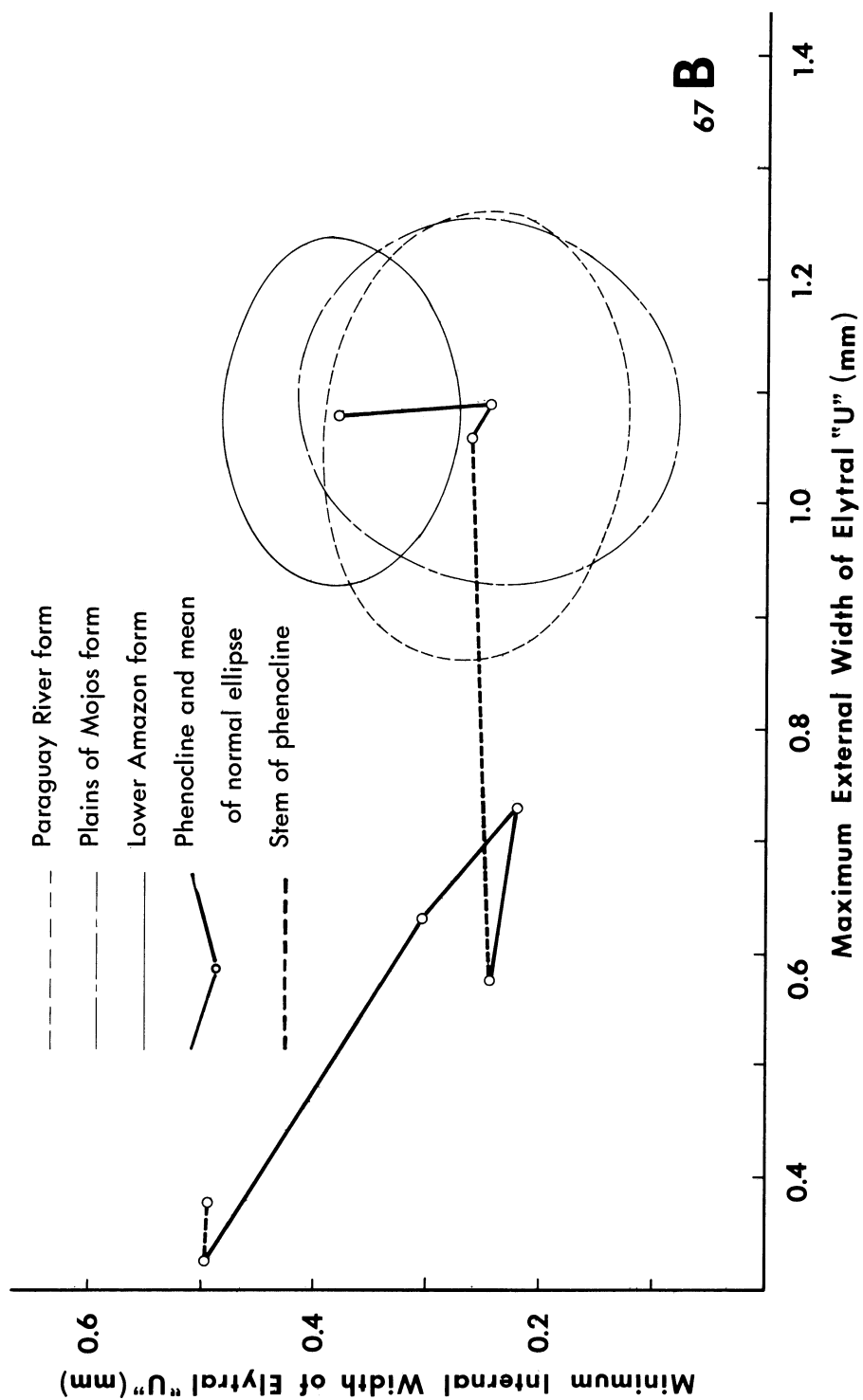


FIGURE 67.—Means and bivariate normal ellipses (second version) for relations in flea beetles between maximum width of the base of the black U-shaped elytral marking and the minimum width of the base of the ivory U-shaped elytral marking. A, Females. B, Males. The solid line connecting the mean points for each subspecific form is the phenocline of the fasciate forms. It is continuous with the phenocline of the vittate species which is shown without normal ellipses. A dashed line connects these two phenoclines and at one end the mean point of *Disomycha argentinensis* to form the second version phenocline.

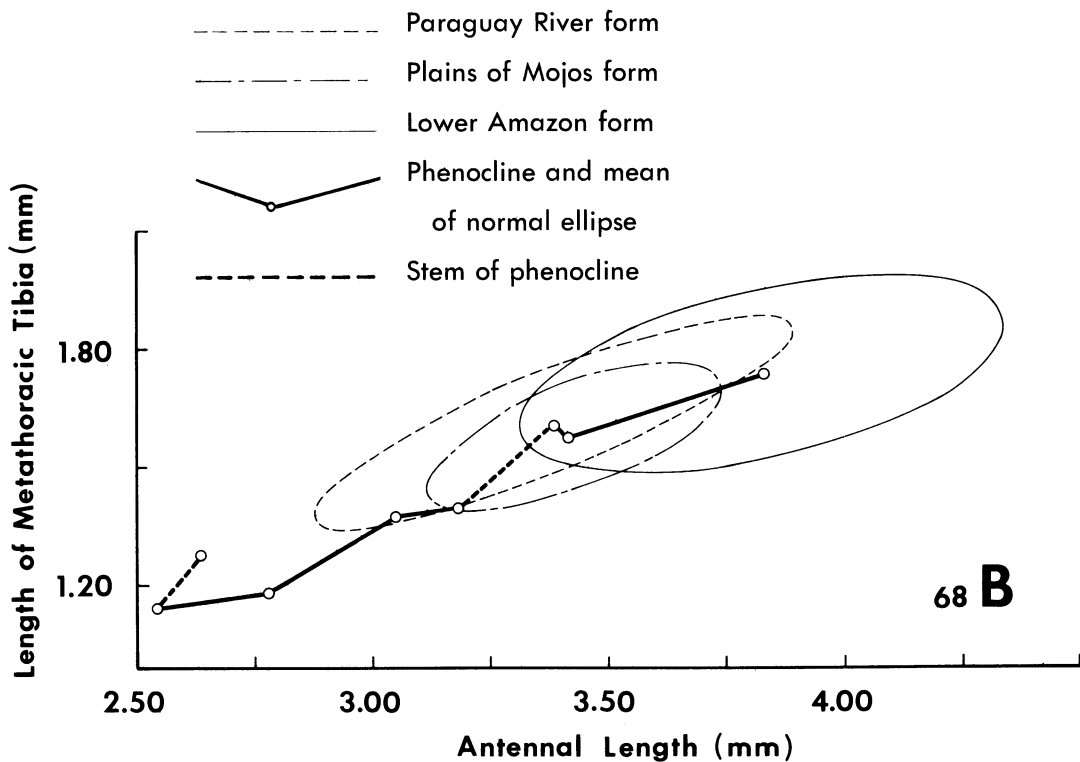
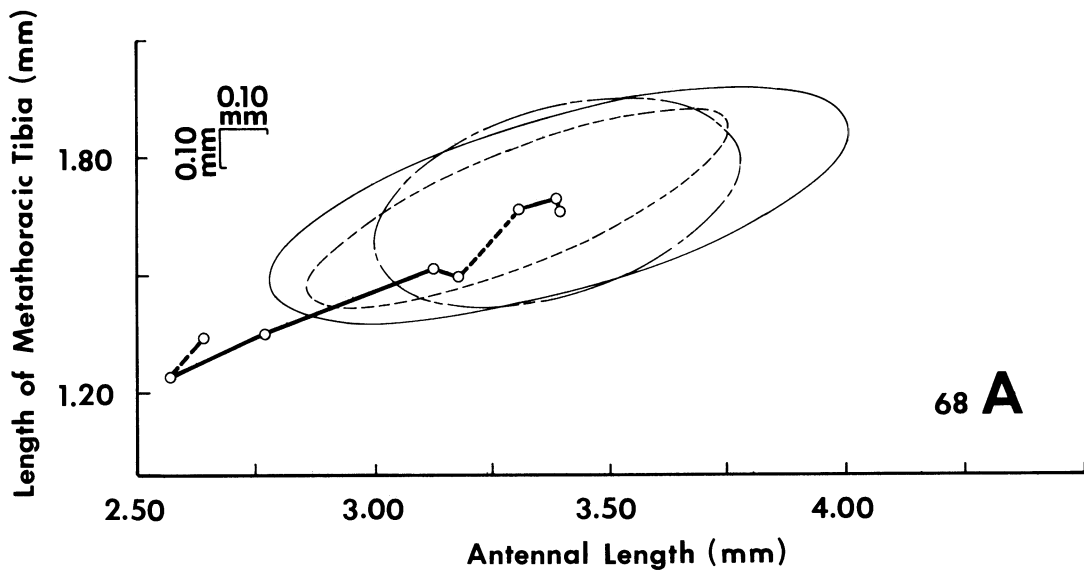


FIGURE 68.—Means and bivariate normal ellipses (second version) for relations in flea beetles between antennal length and metathoracic tibial length. A, Females. B, Males. The solid line connecting the mean points for each subspecific form is the phenocline of the fasciate forms. It is continuous with the phenocline of the vittate species, which is shown without normal ellipses. A dashed line connects these two phenoclines and, at one end, the mean point of *Disonychia argentinensis* to form the second-version phenocline.

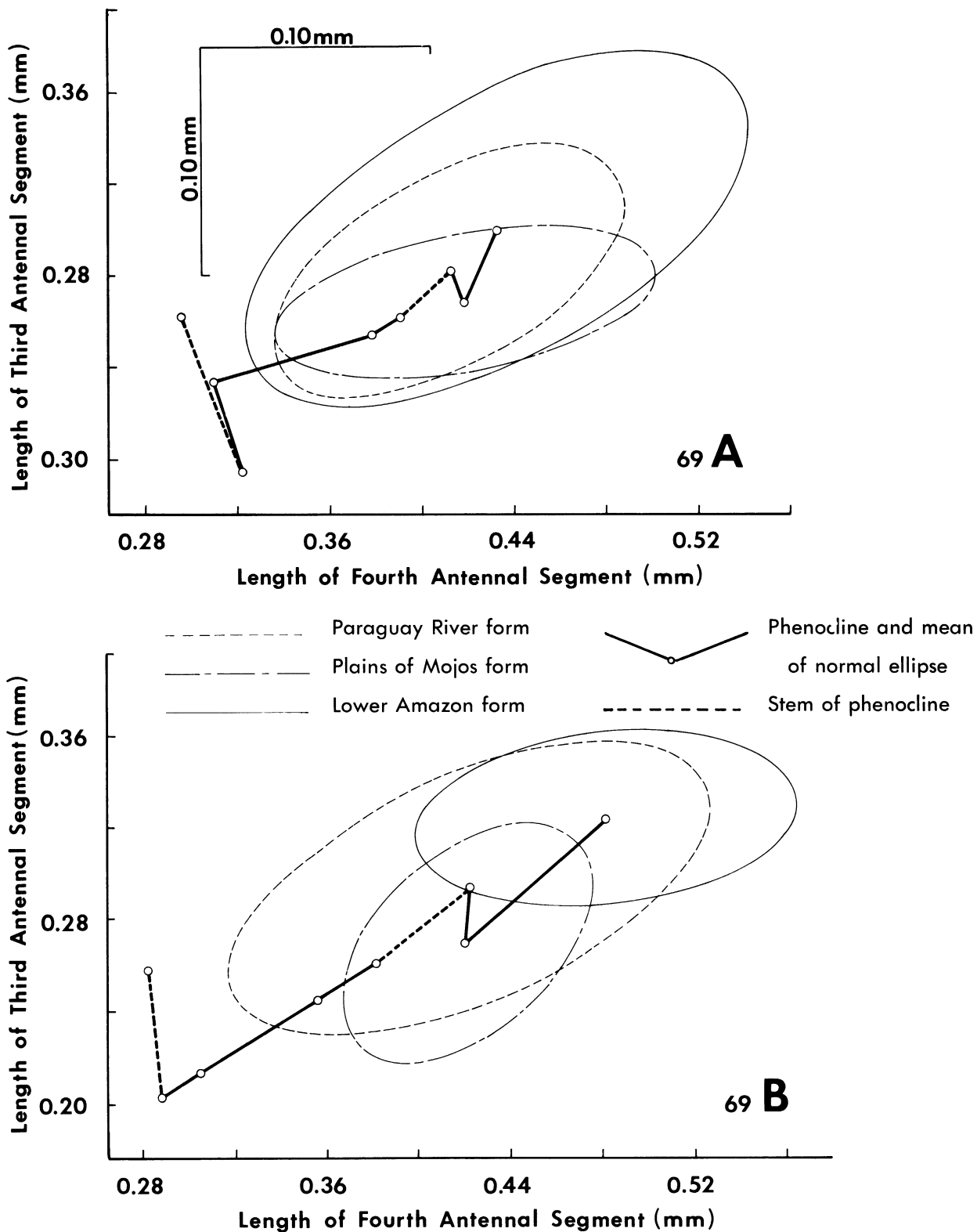
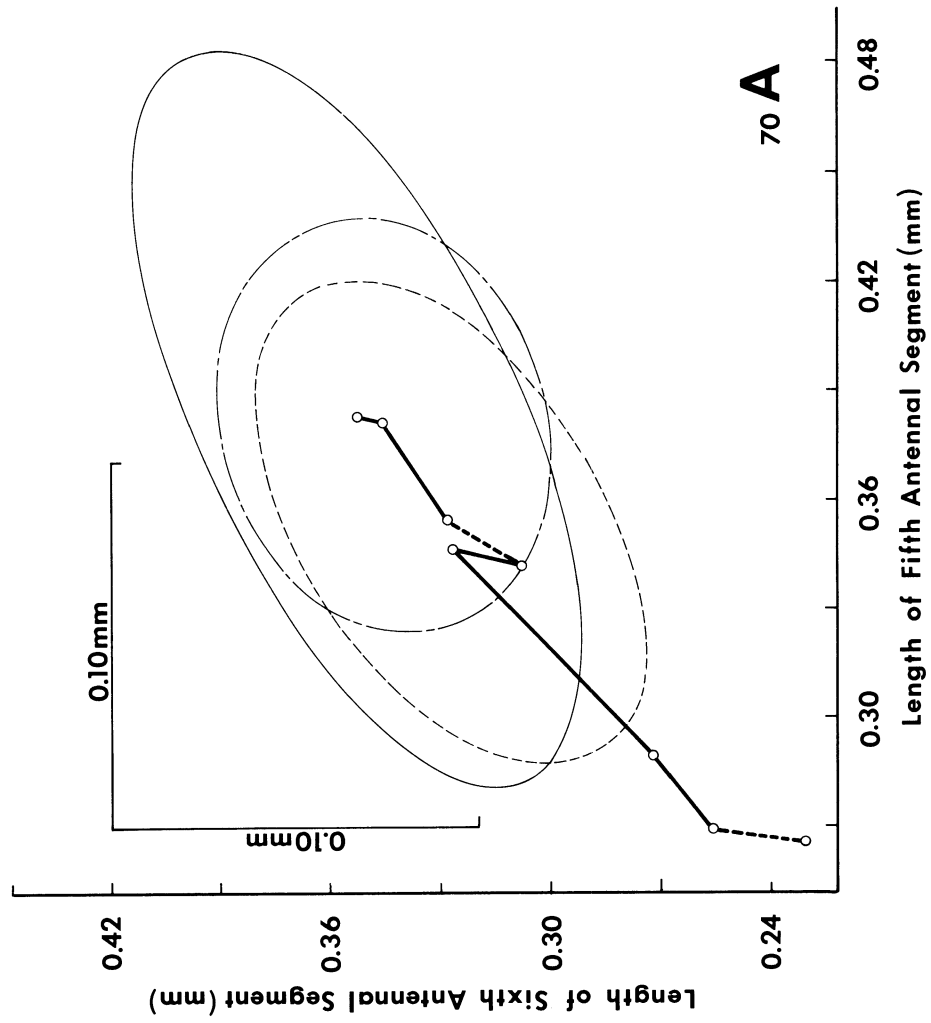


FIGURE 69.—Means and bivariate normal ellipses (second version) for relations in flea beetles between lengths of fourth and third antennal segments. A, Females. B, Males. The solid line connecting the mean points for each subspecific form is the phenocline of the fasciate forms. It is continuous with the phenocline of the vittate species, which is shown without normal ellipses. A dashed line connects these two phenoclines and, at one end, the mean point of *Disonychia argentinensis* to form the second-version phenocline.



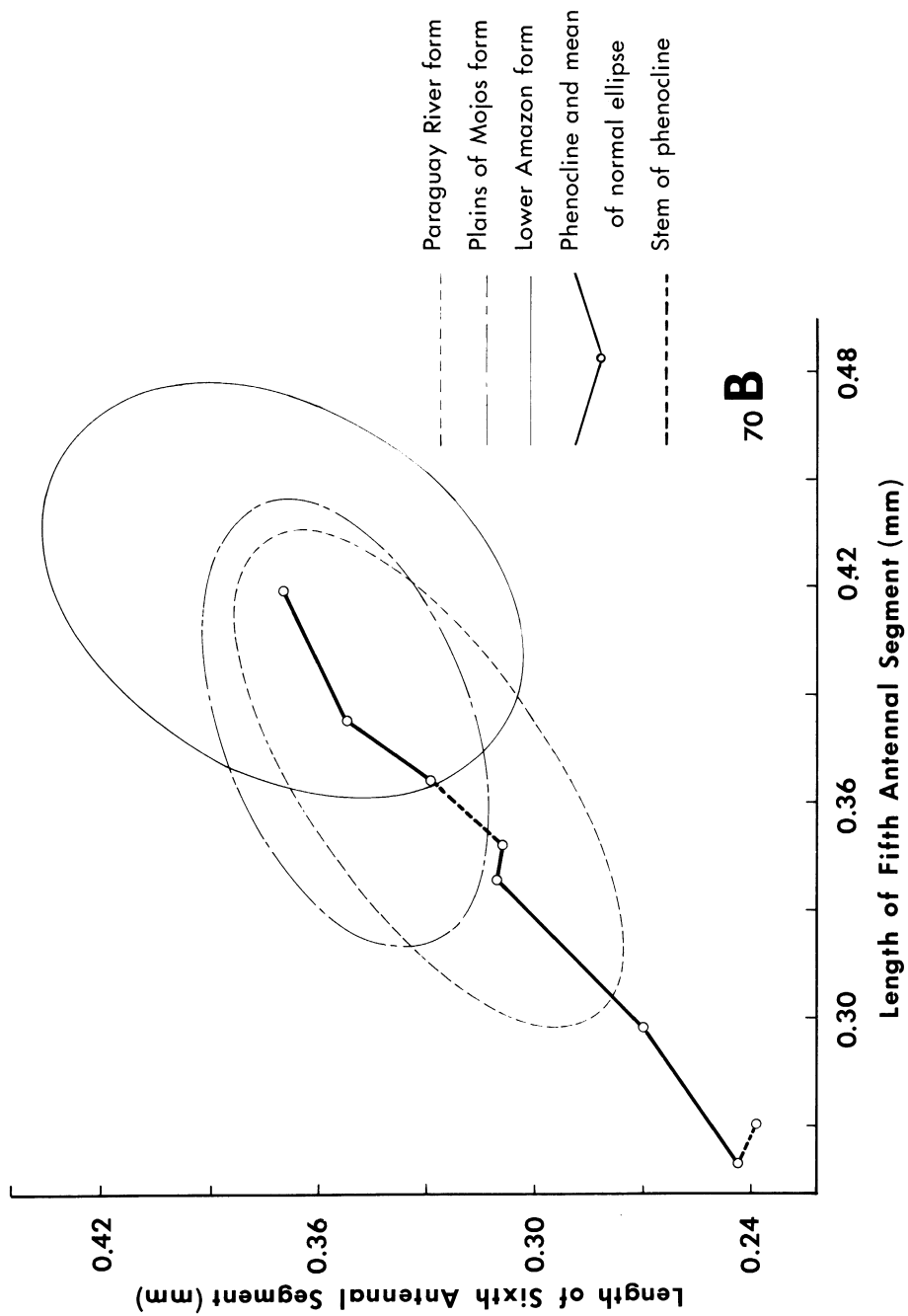
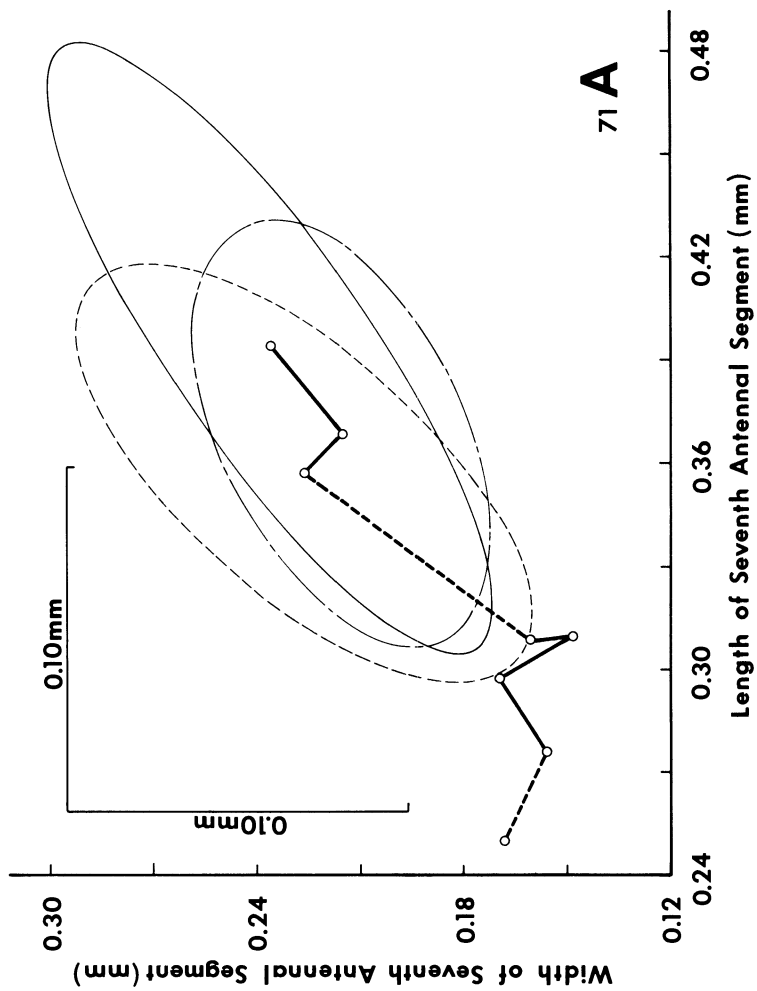


FIGURE 70.—Means and bivariate normal ellipses (second version) for relations in flea beetles between lengths of sixth and fifth antennal segments. A, Females. B, Males. The solid line connecting the mean points for each subspecific form is the phenocline of the fasciate forms. It is continuous with the phenocline of the vittate species, which is shown without normal ellipses. A dashed line connects these two phenoclines and, at one end, the mean point of *Disonychia argentinensis* to form the second-version phenocline.



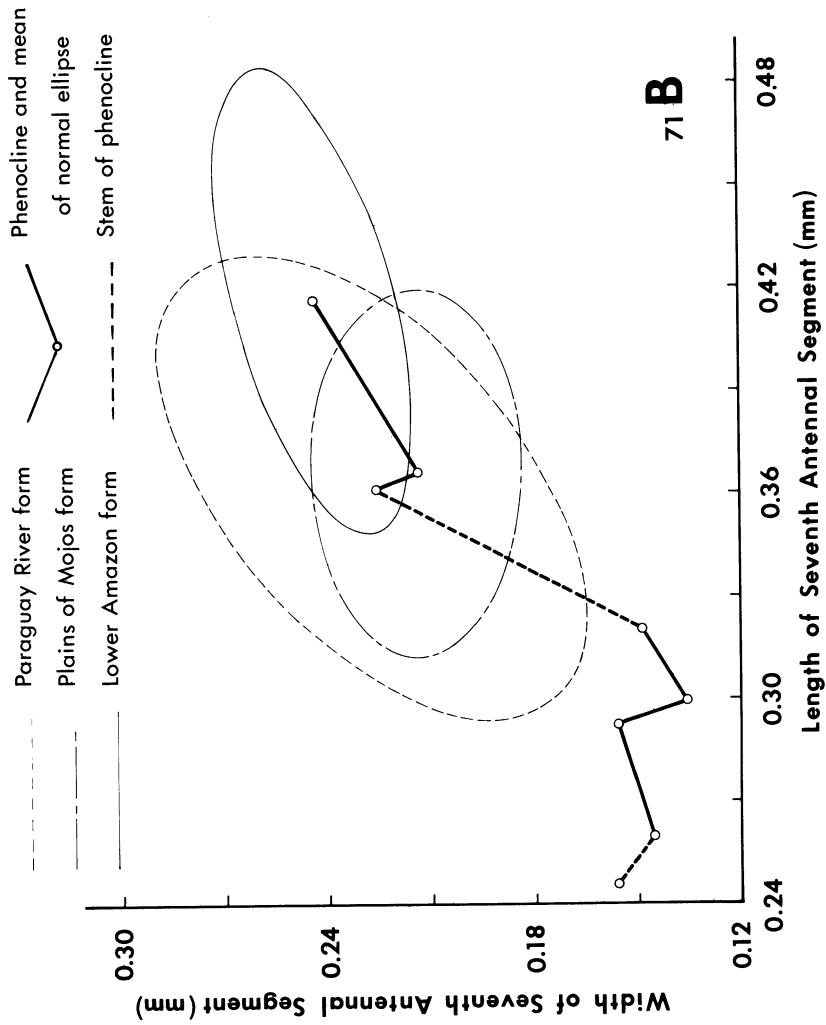
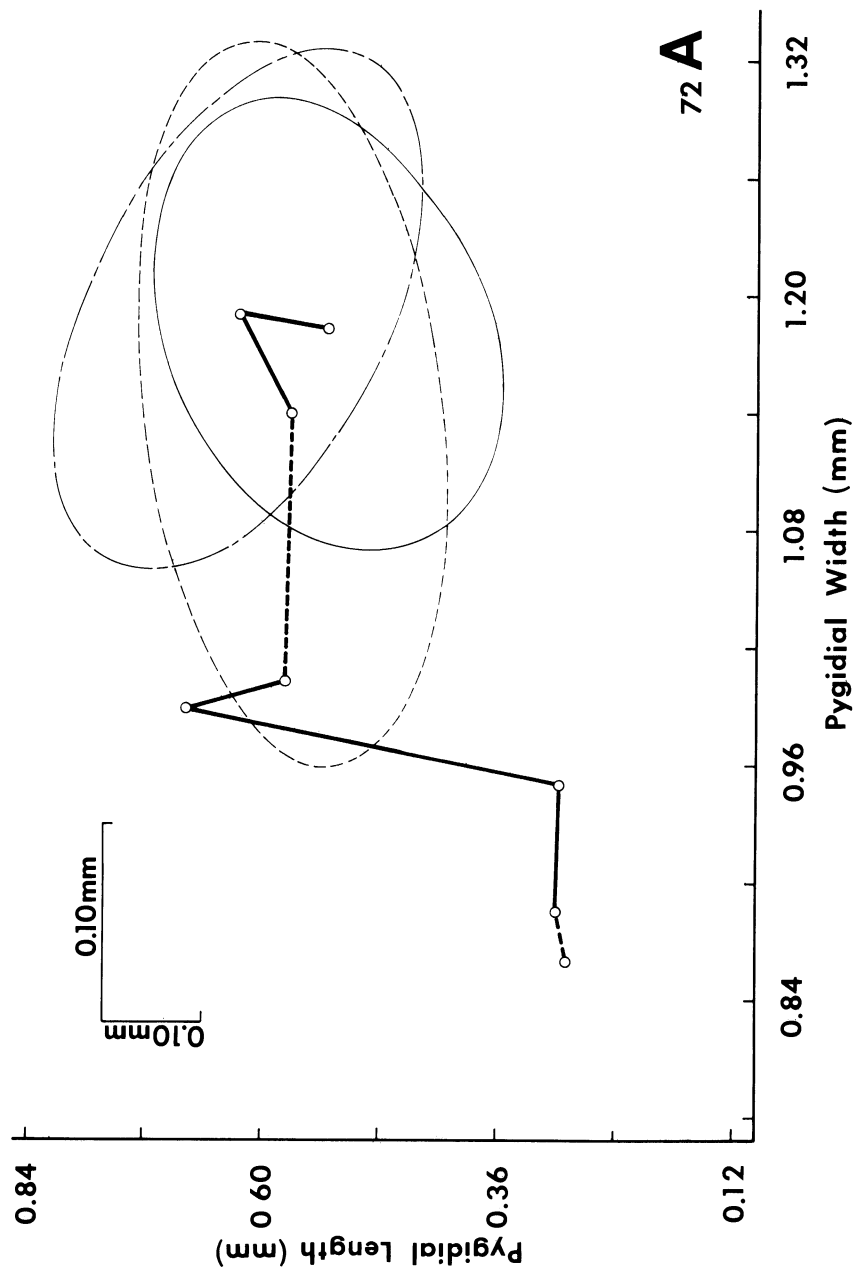


FIGURE 71.—Means and bivariate normal ellipses (second version) for relations in flea beetles between length and width of seventh antennal segment. A, Females. B, Males. The solid line connecting the mean points for each subspecific form is the phenocline of the fasciate forms. It is continuous with the phenocline of the vittate species, which is shown without normal ellipses. A dashed line connects these two phenoclines and, at one end, the mean points of *Disonycha argentinensis* to form the second-version phenocline.



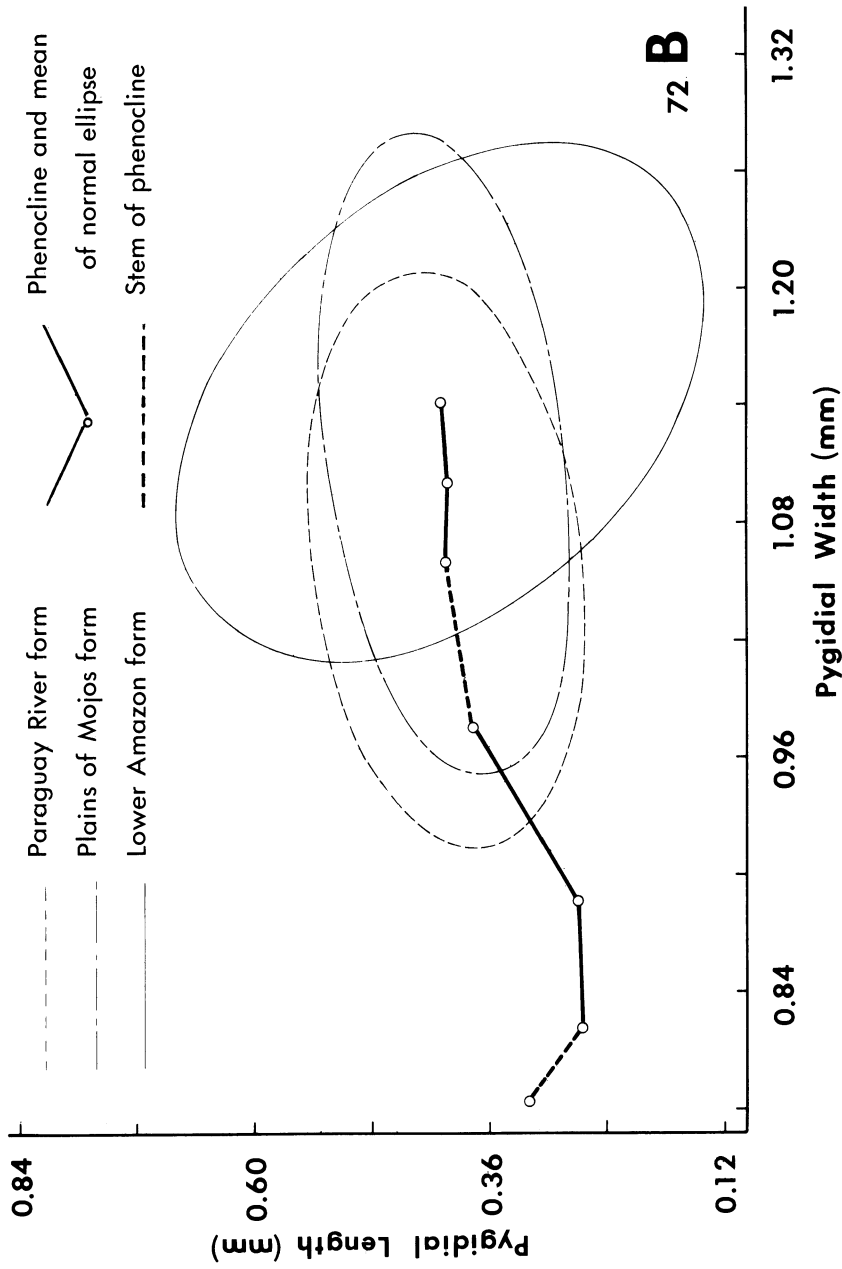


FIGURE 72.—Means and bivariate normal ellipses (second version) for relations in flea beetles between pygidial width and length. A, Females. B, Males. The solid line connecting the mean points for each subspecific form is the phenocline of the fasciate forms. It is continuous with the phenocline of the vittate species, which is shown without normal ellipses. A dashed line connects these two phenoclines and, at one end, the mean point of *Disonychia argentinensis* to form the second-version phenocline.

though the phenoclines are somewhat longer, especially for the females, all three ellipses for both sexes fall narrowly within the pair based on the 1960–61 combined samples (fig. 59).

Figure 72 represents the relationship of pygidial width (PyW) and pygidial length (PyL). As with the vittate species represented in figure 60A, the normal ellipses for females of the three fasciate forms show various angles of orientation and the Plains (Llanos) of Mojós form has a negative coefficient of correlation. Also, as with the vittate species, the phenocline shows sharply changing trends. On the other hand, the males show the marked sexual dimorphism that occurs in the vittate species. It is manifest in a continuation of the rather straight phenocline, which shows little vertical displacement, that is, change in pygidial length. The phenoclines for both sexes are moderately long, but the breadth and large size of the ellipses preclude appreciable taxonomic discrimination. Although the phenoclines have been scaled down to the point of being somewhat smaller than those of the previous section, all three normal ellipses extend appreciably (more so in the males) beyond those based on the combined samples of *Agasicles opaca* (fig. 60). We attribute the larger size of these ellipses to the effects of both the subdivision of the samples into three geographic forms and the increased variance resulting from the 1975 sample supplements.

Table 9 gives the total phenocline distances, as shown in figures 62–72, for the four vittate species of *Agasicles* and for the three fasciate forms of *A. opaca*. The sum of the distances taken up by the vittates for all character pairs comprises 70 percent of the overall *Agasicles* phenoclinical distances for females and 59 percent for males. However, the mean intermean point distances are relatively less, with only 60 percent of the sums for females and 49 percent for males. These results indicate that the intermean point distances of the vittate forms are greater, on the average, for females and subequal, on the average, for the males as compared with the fasciates. For each character pair, we also present in table 9 the percentage of the total *Agasicles* phenocline taken up by the vittate species. These percentages range from 54 to 86 for the females and 49 to 70 for the males. These results show that the phenoclines for the vittates are longer than those of the fasciates for all character pairs except for PrW to PrL and BL to BTh being a trifle shorter in the males. However, percentages based on the means of the intermean point distances show that the vittates extend less than 50 percent of

the distance along the *Agasicles* phenocline for two character pairs in the females and seven in the males. For the females, the percentages range from 43 to 79 and for the males from 38 to 71. Later (p. 104), we will find that the order of the mean points of the third-version phenoclines results in the vittates exceeding the fasciates for all character pairs but three. These are judgmental comparisons, not statistical statements, because of the small sample size.

Table 10 gives the successive phenoclinical distances between mean points of the character pairs (intermean point distances) for the vittate and fasciate *Agasicles* and *Disonycha argentinensis* as shown in figures 62–72. The totals of the intermean point distances between the most derived vittate, *A. vittata*, and the least derived fasciate Paraguay River form of *A. opaca* are 723 (31 percent) for the females and 702 (31 percent) for the males. These exceed by far all other totals given in table 10 and represent the widest evolutionary divergence along the phenocline. However, the distances are not maximal for 4 of the 11 character pairs, namely, AL to MTL, 4AL to 3AL, 6AL to 5AL, and PyW to PyL. Each of these is surpassed by one to four of the other five *Agasicles* intermean point distances. Among the vittate *Agasicles* species the phenoclinical distances between *A. interrogationis* and *A. vittata* are the shortest, both for females and males and for all 11 character pairs except PyW to PyL (males only) and U2W to U1W. Since biogeographic evidence indicates clearly that these two species are at opposite ends of a long series of geographic forms (fig. 34), we must consider their apparent similarity to have resulted from evolutionary convergence. Among the fasciate forms, the phenoclinical distance between the Paraguay River form and the Plains of Mojós form of *Agasicles opaca* is even less than that between *A. interrogationis* and *A. vittata*. But in this case, geographic contiguousness enables us to interpret phenoclinical proximity as indicating true affinity. However, the closely related lower Amazon River form is widely separated phenoclinally, indicating wide divergence but with geographic proximity and general similarity indicating close affinity.

In table 10, the female-to-female-plus-male percentages, based on the totals both by intermean point distance and by character pair, do not show sexual dimorphism clearly. However, the two sets of values for the obviously sexually dimorphic PyW to PyL do show the largest percentage of difference between females and males, though only by a small

Table 9.—Total second-version phenocline distances for vittate species of *Agasicles* and for geographic forms of fasciate *A. opaca* as shown in figures 62–72

Character pair (<i>x</i> to <i>y</i>)	Vittate <i>A. hygrophila</i> to <i>A. vittata</i> (mm)		Fasciate <i>A. opaca</i> (Paraguay River form to Amazon River form) (mm)		Percent vittate distance, <i>A. hygrophila</i> to <i>A. opaca</i> (lower Amazon River form)	
	Total	Intermean point (mean <i>n</i> =3)	Total	Intermean point (mean <i>n</i> =2)	Total	Intermean point
FEMALES						
PrW to PrL (fig. 62)	72	24	33	17	69	59
EL to EW (fig. 63)	49	16	38	19	56	46
BL to BTh (fig. 64)	58	19	50	25	54	43
HW to HL (fig. 65)	47	16	20	10	70	62
IOW to IAW (fig. 66)	63	21	29	15	69	58
U2W to U1W (fig. 67)	166	56	60	30	74	65
AL to MTL (fig. 68)	67	22	11	6	86	79
4AL to 3AL (fig. 69)	81	27	30	15	73	64
6AL to 5AL (fig. 70)	105	35	33	16	76	69
7AL to 7AW (fig. 71)	52	17	41	21	56	45
PyW to PyL (fig. 72)	133	44	44	22	75	67
Total	893	298	390	196	—	—
Percent	70	60	30	57	70	60
MALES						
PrW to PrL (fig. 62)	59	19	61	31	49	38
EL to EW (fig. 63)	51	17	45	23	53	43
BL to BTh (fig. 64)	31	10	32	16	49	38
HW to HL (fig. 65)	24	8	23	12	51	40
IOW to IAW (fig. 66)	55	18	38	19	59	49
U2W to U1W (fig. 67)	163	54	43	22	79	71
AL to MTL (fig. 68)	71	25	49	25	59	50
4AL to 3AL (fig. 69)	70	23	68	34	51	40
6AL to 5AL (fig. 70)	97	32	58	29	63	53
7AL to 7AW (fig. 71)	68	23	62	31	52	43
PyW to PyL (fig. 72)	77	26	34	17	70	61
Total	766	255	513	259	—	—
Percent	59	49	40	51	59	49

margin. Generally, the totals on which these percentages are based obscure the sexually dimorphic changes that are usually localized in individual intervals of the phenoclines. A more definitive measure of sexual dimorphism may therefore be the female percentage of the combined female and male distances between each of the phenoclinal mean points given in table 10. These percentages indicate the differences in rates of change between females and males for a particular interval of the phenocline pair. We give these percentages separately in table 11 for females only and arbitrarily consider values above 65 percent and below 35 percent as being indicative of evolutionary trends that are sexually dimorphic. In table 11 the indicative percentages are starred. They show a rather scattered distribu-

tion. Seven of the eleven character pairs include from one to three percentages considered as indicating sexual dimorphism. Previously, we considered phenoclines of four of these character proportions as exhibiting sexual dimorphism (page 74). From the standpoint of phenoclinal intermean point distances, two intervals (*Agasicles vittata* to Paraguay River form of *A. opaca* and Paraguay River form to Plains of Mojós form of *A. opaca*) have no percentages considered as being indicative. A single interval, *Agasicles connexa* to *A. interrogationis*, has two; another, *A. hygrophila* to *A. connexa* includes three; and the Plains of Mojós to lower Amazon interval includes four. The largest number of percentages considered to be indicative (six) occur within the *Agasicles interrogationis* to *A. vittata*

Table 10.—Successive second-version phenocline distances between mean points of character pairs for vittate and fasciate *Agasicles* species and *Disorycha argentinensis* as shown in figures 62–72
[Millimeters]

Character pair (<i>x</i> to <i>y</i>)	<i>D. argen- tinensis</i> to <i>A. hy- grophila</i>	<i>A. hygro- phila</i> to <i>A. con- nera</i>	<i>A. connera</i> to <i>A. inter- rogationis</i>	<i>A. interroga- tionis</i> to <i>A. vittata</i>	<i>A. vittata</i> to Paraguay River form of <i>A. opaca</i>	Paraguay River form to Plains of Mojos form of <i>A. opaca</i>	Plains of Mojós form to lower Amazon River form of <i>A. opaca</i>	<i>A. hygrophila</i> to lower Amazon River form of <i>A. opaca</i>	
								Total	Percent ♀ / ♂ + ♂
FEMALES									
PrW to PrL (fig. 62)	112	51	13	8	139	14	19	244	49
EL to EW (fig. 63)	15	19	26	4	65	5	33	152	50
BL to BTh (fig. 64)	2	19	31	8	44	7	43	152	58
HW to HL (fig. 65)	32	17	16	14	53	3	17	120	55
IOW to IAW (fig. 66)	60	23	27	13	98	10	19	190	50
U2W to U1W (fig. 67)	7	87	35	44	139	12	48	365	53
AL to MTL (fig. 68)	11	22	39	6	19	9	3	98	40
4AL to 3AL (fig. 69)	46	26	46	9	19	9	21	130	43
6AL to 5AL (fig. 70)	21	23	66	16	20	27	6	159	48
7AL to 7AW (fig. 71)	24	21	21	10	69	13	28	162	48
PyW to PyL (fig. 72)	11	28	83	22	58	24	20	235	62
Total	341	336	403	154	723	133	257	—	—
Percent	15	14	17	7	31	6	11	—	—
Percent ♀ / ♂ + ♂	56	53	60	46	51	50	40	—	—
MALES									
PrW to PrL (fig. 62)	92	42	10	7	136	23	38	256	51
EL to EW (fig. 63)	16	16	32	3	55	5	40	151	50
BL to BTh (fig. 64)	4	8	21	2	48	5	27	111	42
HW to HL (fig. 65)	19	14	8	2	53	7	16	100	45
IOW to IAW (fig. 66)	37	16	21	18	95	9	29	188	50
U2W to U1W (fig. 67)	13	91	33	39	122	9	34	328	47
AL to MTL (fig. 68)	15	25	32	14	27	5	44	147	60
4AL to 3AL (fig. 69)	36	13	38	19	33	16	52	171	57
6AL to 5AL (fig. 70)	10	39	49	9	23	24	34	178	52
7AL to 7AW (fig. 71)	15	29	18	21	74	12	50	204	52
PyW to PyL (fig. 72)	14	6	27	44	36	17	17	147	38
Total	271	299	289	178	702	135	381	—	—
Percent	12	13	13	8	31	6	17	—	—
Percent ♀ / ♂ + ♂	45	48	42	54	50	51	61	—	—

Table 11.—Female percentages of the combined female and male distances between each of the phenoclineal mean points given in table 10 for seven forms of *Agasicles*. Percentages above 65 and those 35 or below are considered indicative of a sexually dimorphic trend and are starred

Character pair (x to y)	<i>D. argentinensis</i> to <i>A. hygrophila</i>	<i>A. hygrophila</i> to <i>A. connexa</i>	<i>A. connexa</i> to <i>A. interrogans</i>	<i>A. interrogans</i> to <i>A. vittata</i>	<i>A. vittata</i> to Paraguay River form of <i>A. opaca</i>	Paraguay River form to Plains form of <i>A. opaca</i>	Plains of Mojos form to lower Amazon River form of <i>A. opaca</i>
PrW to PrL (fig. 62)	55	55	52	53	51	38	33*
EL to EW (fig. 63)	48	54	45	57	54	50	45
BL to BTh (fig. 64)	33*	71*	60	80*	48	58	61
HW to HL (fig. 65)	63	55	67*	87*	50	30	52
IOW to IAW (fig. 66)	62	59	55	42	51	53	40
U2W to U1W (fig. 67)	35*	49	51	54	53	57	59
AL to MTL (fig. 68)	42	47	55	33*	41	64	6*
4AL to 3AL (fig. 69)	56	67*	55	32*	37	36	29*
6AL to 5AL (fig. 70)	68*	37	57	64	47	53	15*
7AL to 7AW (fig. 71)	62	42	54	32*	48	52	36
PyW to PyL (fig. 72)	44	82*	75*	33*	62	59	54

interval. But these values are probably invalid because, as noted above and on pages 74 and 87, a more remote relationship between these two species may not allow them to be placed consecutively on an unbranched phenocline as represented by the first and second versions presented thus far.

Proposed trifurcate representation for the phenoclines

Except along the eastern littoral and adjacent escarpments, Müller (1973) and Haffer (1974) report no forested refugia in northeastern Brazil during the arid climatic periods of the Pleistocene (figs. 86 and 87). We also find a void in the distribution of both alligatorweed and *Agasicles* across northeastern Brazil to Belém. For the vittate *Agasicles* species the hiatus continues to Georgetown and up the Amazon River beyond Manaus. This wide separation between *Agasicles interrogationis* and *A. vittata* is consistent with an out-of-line (switchback) position for *A. vittata* on several phenoclines, most notably for two plottings: elytral length (EL) against elytral width (EW) and the maximum width of the base of the black U-shaped elytral marking (U2W, fig. 46) against the minimum width of the base of the ivory U-shaped elytral markings (U1W, fig. 46). The rather wide divergence between the fasciate forms of *Agasicles* and the vittate forms is evident in the contrast in configuration and color of their markings and by the wide separation between their points along the phenoclines generally. The Paraguay River form of fasciate *Agasicles opaca* overlaps the range of vittate *A. hygrophila* and is allopatric with the two Amazonian forms. These facts indicate that the Recent species of *Agasicles* do not constitute an unbranched phenocline or a closed circle of closely related forms but rather a trifurcate series, shown diagrammatically in fig. 73.

Based on this representation, we present in figures 74–84 corresponding trifurcate phenoclines for each of the 11 sets of character pairs considered in the previous two sections. These third-version phenoclines are at the same scale as those of the second version presented in figures 62–72. Each set is composed of a representation for the females (A) and for the males (B). For each phenocline the mean point of *Agasicles hygrophila* is the center from which radiate the stem leading from *Disonychia argentinensis* (Da) and the three arms, each terminating in a mean point of an *Agasicles* species as follows: vittate *A. vittata* (Av), vittate *A.*

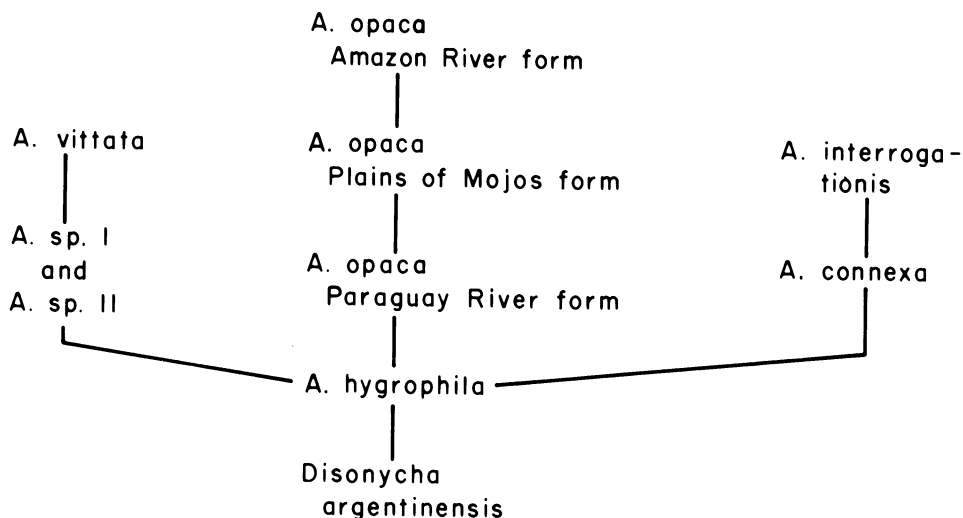


FIGURE 73.—Trifurcate representation of relationship of existing *Agasicles* species. This scheme is consistent with the progression rule and the rule of deviation as proposed by Hennig (1966). The representation is superimposable upon existing geographical ranges. Although we proposed species I and II, we no longer consider them as unknown existing intermediate forms between *Agasicles vittata* and *A. hygrophila*.

interrogationis (Ai), and fasciate lower Amazon River form of *A. opaca* (Aoa).

Figures 74–84 clearly show that, for all 11 character pairs, the phenoclinal arm terminating in the lower Amazon form of *Agasicles opaca* (Aoa) is significantly longer than the other two, denoting much greater increase in size. The phenoclinal arm terminating in vittate *A. vittata* (Av) is somewhat shorter to subequal to that terminating in vittate *A. interrogationis* (Ai) except for character pairs PyW to PyL (males only), AL to MTL, and 4AL to 3AL. The phenoclinal stem leading from *Disonycha argentinensis* is shorter than the arms for the vittate *Agasicles* except for three character pairs (in order of decreasing magnitude): PrW to PrL, IOW to IAW, and HW to HL. In table 12, we tabulate the lengths of the stem and the three arms for each character pair. Generally, the values for the *Disonycha argentinensis* stem are irregular to discordant in comparison with the usual trend of increasing lengths proceeding from the *Agasicles vittata* arm to the *A. interrogationis* arm to lower Amazon form of the *A. opaca* arm. The totals for both females and males show more dramatically this trend of increasing values among *Agasicles* and also the *Disonycha argentinensis* stem as the shortest of the two sets of four totals.

In figures 74–84, another feature of the trifurcate representation having the mean point of *Agasicles hygrophila* as its center are the sizes of the angle of the stem and of the angles of radiation of the three arms with respect to the stem. The angles are

formed by the slopes of the stem and each of the arms and express degrees of divergence of one member with respect to the stem. The spread of angles is greatest for the character pair IOW to IAW. It is least for the arms for 6AL to 5AL and BL to BTh. In seven of the charts this spread tends to be small for the three arms, indicating concordance in evolutionary change. Striking changes in direction along the arms occur and may signify corresponding changes in evolutionary course, probably in response to change in selection pressure.

Table 13 gives the phenoclinal distances for Recent vittate and fasciate *Agasicles* species as shown in figures 74–84. The distances for the fasciates remain unchanged from the previous representations of the second-version phenoclines. However, in the third version, representation of *Agasicles vittata* as a separate arm increases the phenoclinal distances for the vittate *Agasicles* for all character pairs except two. These are HW to HL and IOW to IAW, and there is a decrease in these because of the separate arms being slightly shorter than the intervals of the second-version phenocline that they replace.

In the trifurcate representation (table 13), the distances taken up by the vittates are longer for all character pairs than those of the fasciates, ranging from 59 to 92 percent (average 75 percent) of the total *Agasicles* phenoclinal distance for the females and 52 to 83 percent (average 69 percent) for the males. The mean intermean point distances are not

(Continued on page 117.)

Table 12.—Lengths of stem and 3 arms of the proposed trifurcate phenocline as expressed by each of the 11 character pairs. The mean point for *Agasicles hygrophila* is central for each phenocline shown in figures 74–84 (third-version phenoclines)

Distance from mean point of <i>A. hygrophila</i> to mean point of—										
Character pair (<i>x</i> to <i>y</i>)	Female <i>D. argen- tinensis</i> (stem)	Female <i>A. vittata</i> (arm)	Female <i>A. inter- rogationis</i> (arm)	Female lower Amazon River form of <i>A. opaca</i> (arm)	Male <i>D. argen- tinensis</i> (stem)	Male <i>A. vittata</i> (arm)	Male <i>A. inter- rogationis</i> (arm)	Male lower Amazon River form of <i>A. opaca</i> (arm)		
PrW to PrL (fig. 74)	112	45	51	216	92	40	53	236		
EL to EW (fig. 75)	15	40	45	139	17	47	48	145		
BBL to BTh (fig. 76)	2	43	30	135	4	31	30	110		
HW to HL (fig. 77)	32	11	33	82	19	8	22	85		
IOW to LAW (fig. 78)	61	10	50	121	37	5	36	131		
U2W to U1W (fig. 79)	7	85	123	273	13	90	124	144		
AL to MTL (fig. 80)	12	66	62	96	15	69	55	143		
4AL to 3AL (fig. 81)	46	60	71	113	35	70	51	171		
6AL to 5AL (fig. 82)	21	75	88	127	11	93	88	174		
7AL to 7AW (fig. 83)	22	28	42	132	15	51	45	171		
PyW to PyL (fig. 84)	11	76	109	162	14	71	33	152		
Total	341	539	709	1,596	272	575	585	1,662		

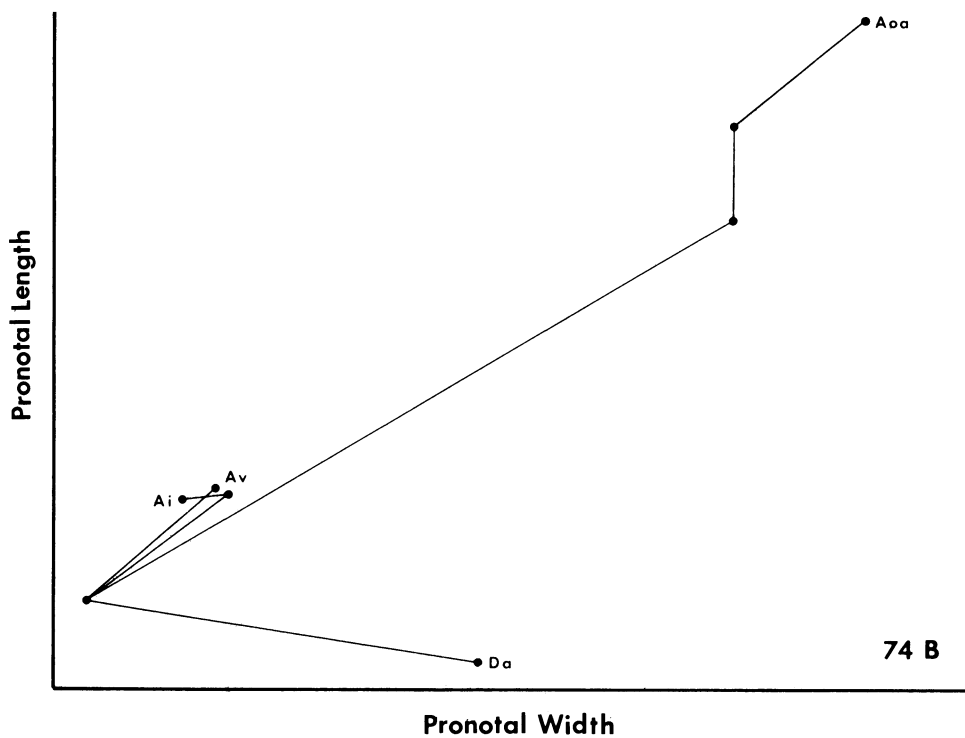
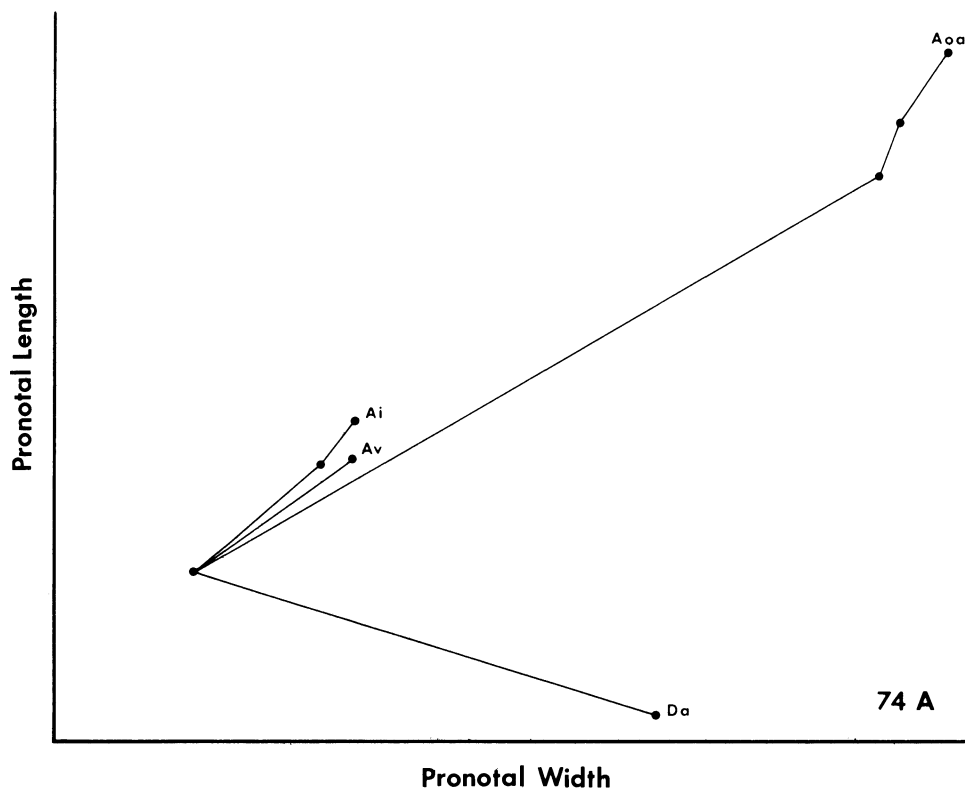


FIGURE 74.—Trifurcate (third-version) phenocline for the mean points of pronotal width to pronotal length of flea beetles. A, Females. B, Males. This phenocline is at the same scale as that of the second version presented in figure 62. The mean point of *Agasicles hygrophila* is the center to which the stem leads from *Disonycha argentinensis* (Da) and from which radiate the three arms, each terminating in a mean point of an *Agasicles* species as follows: vittate *A. vittata* (Av), vittate *A. interrogationis* (Ai), and fasciate lower Amazon River form of *A. opaca* (Aoa).

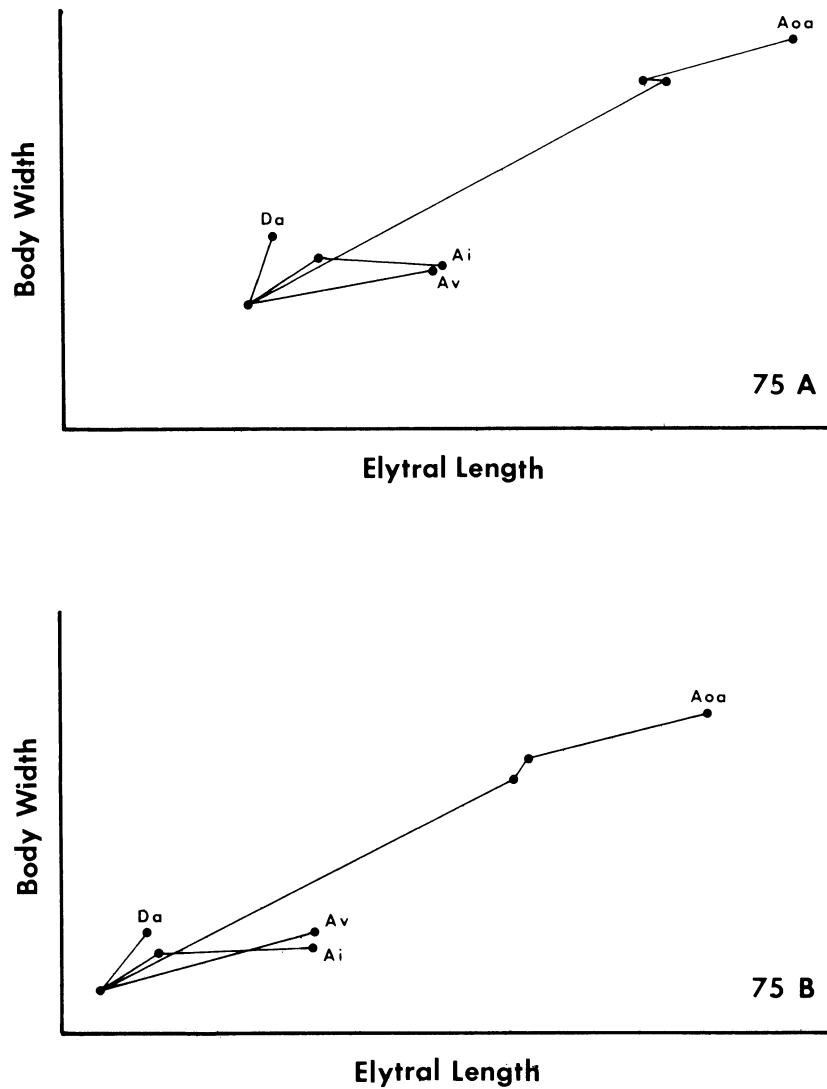


FIGURE 75.—Trifurcate (third-version) phenocline for the mean points of elytral length to elytral width of flea beetles. A, Females. B, Males. This phenocline is at the same scale as that of the second version presented in figure 63. The mean point of *Agasicles hygrophila* is the center to which the stem leads from *Disonycha argentinensis* (*Da*) and from which radiate the three arms, each terminating in a mean point of an *Agasicles* species as follows: vittate *A. vittata* (*Av*), vittate *A. interrogationis* (*Ai*), and fasciate lower Amazon River form of *A. opaca* (*Aoa*).

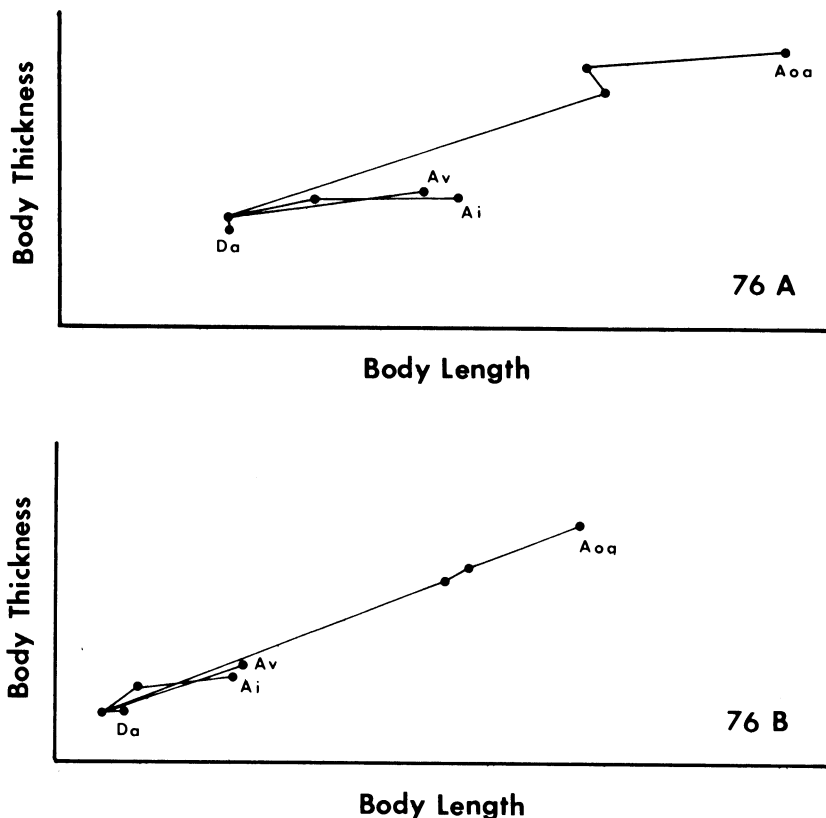


FIGURE 76.—Trifurcate (third-version) phenocline for the mean points of total body length to body thickness of flea beetles. A, Females. B, Males. This phenocline is at the same scale as that of the second version presented in figure 64. The mean point of *Agasicles hygrophila* is the center to which the stem leads from *Disonycha argentinensis* (Da) and from which radiate the three arms, each terminating in a mean point of an *Agasicles* species as follows: vittate *A. vittata* (Av), vittate *A. interrogationis* (Ai), and fasciate lower Amazon River form of *A. opaca* (Aoa).

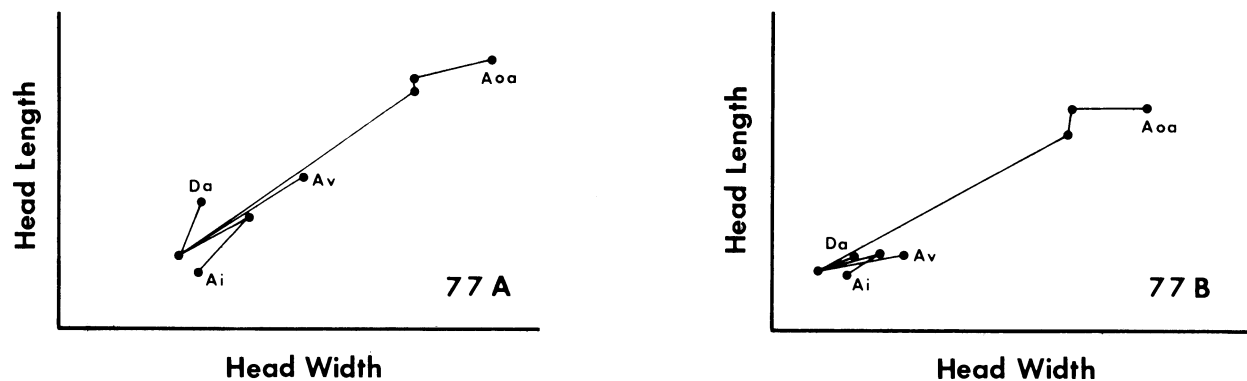


FIGURE 77.—Trifurcate (third-version) phenocline for the mean points of head width to head length of flea beetles. A, Females. B, Males. This phenocline is at the same scale as that of the second version presented in figure 65. The mean point of *Agasicles hygrophila* is the center to which the stem leads from *Disonycha argentinensis* (Da) and from which radiate the three arms, each terminating in a mean point of an *Agasicles* species as follows: vittate *A. vittata* (Av), vittate *A. interrogationis* (Ai), and fasciate lower Amazon River form of *A. opaca* (Aoa).

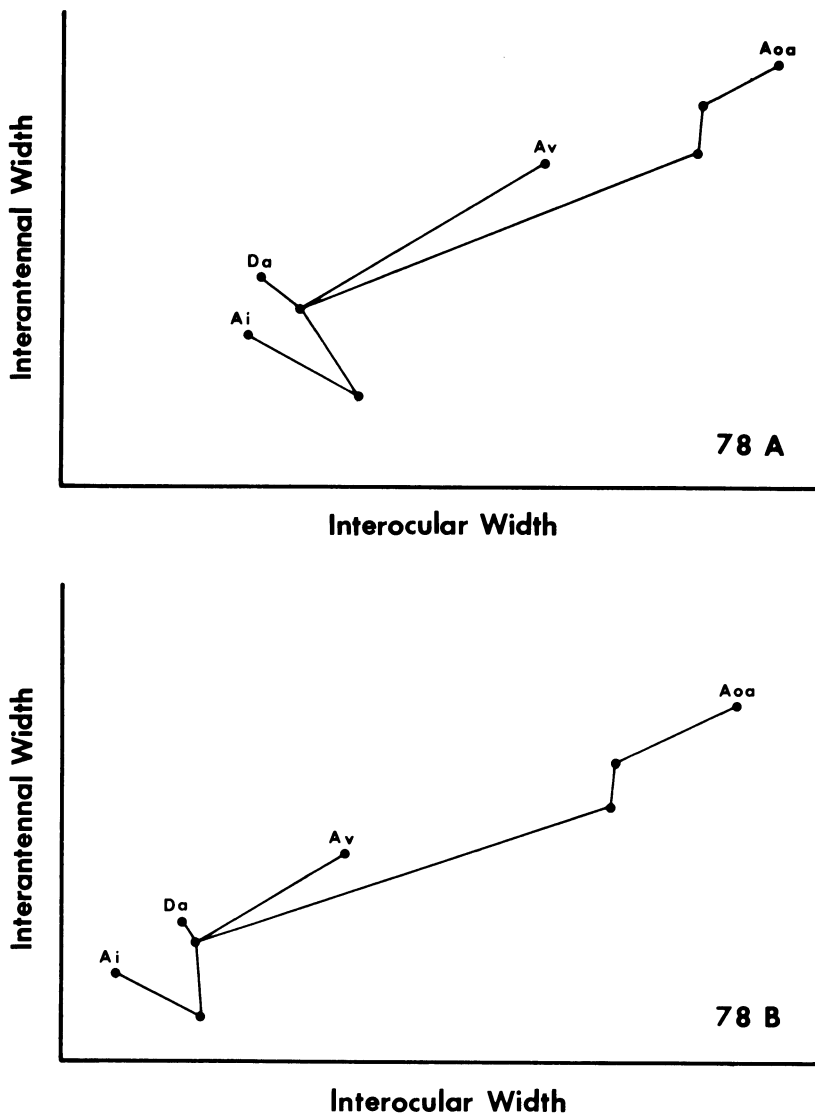


FIGURE 78.—Trifurcate (third-version) phenocline for the mean points of interocular width to interantennal width of flea beetles. A, Females. B, Males. This phenocline is at the same scale as that of the second version presented in figure 66. The mean point of *Agasicles hygrophila* is the center to which the stem leads from *Disonycha argentinensis* (Da) and from which radiate the three arms, each terminating in a mean point of an *Agasicles* species as follows: vittate *A. vittata* (Av), vittate *A. interrogationis* (Ai), and fasciate lower Amazon River form of *A. opaca* (Aoa).

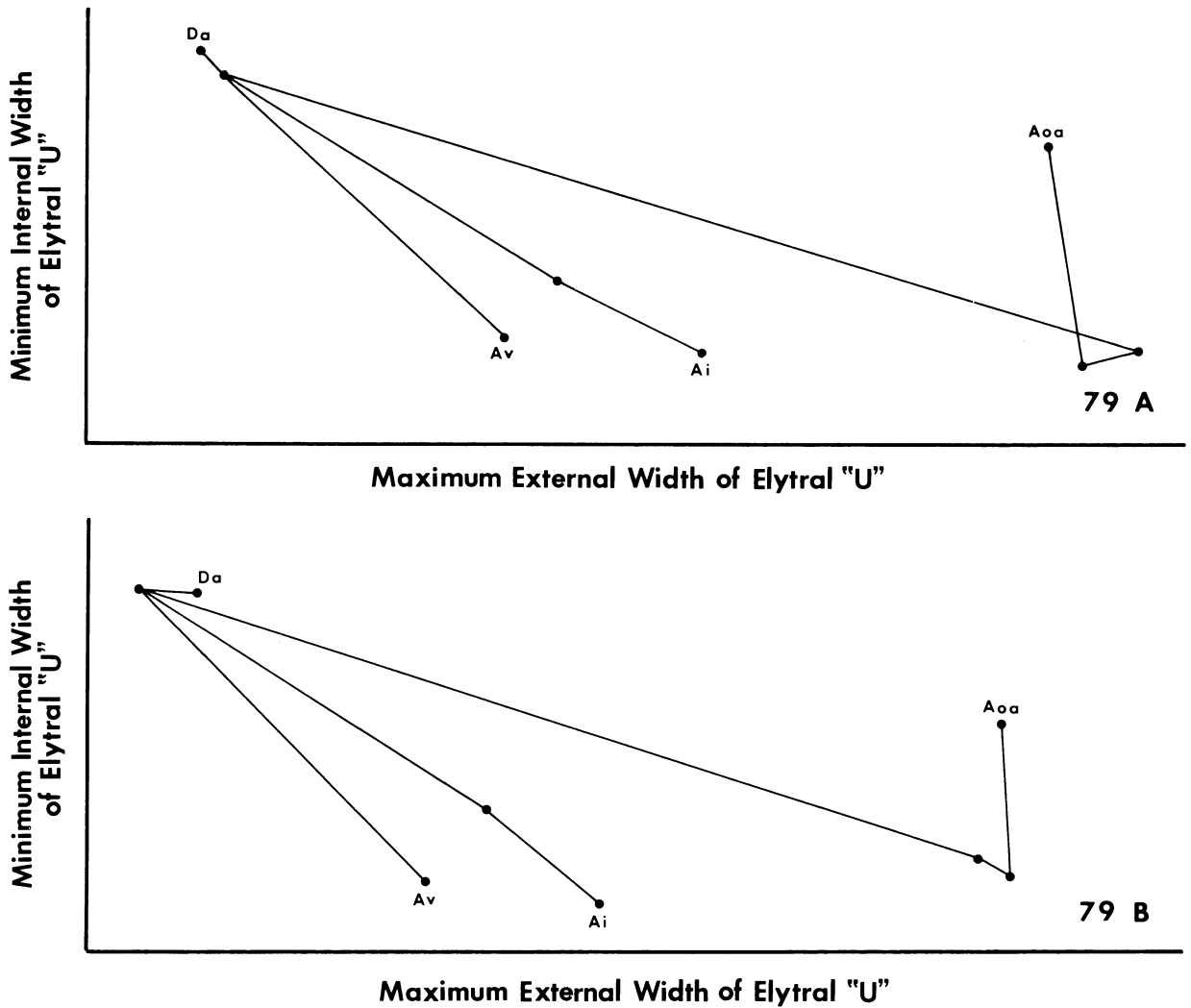


FIGURE 79.—Trifurcate (third-version) phenocline for the mean points of maximum width of the base of the black U-shaped elytral marking to the minimum width of the base of the ivory-colored U-shaped elytral marking of flea beetles. A, Females. B, Males. This phenocline is at the same scale as that of the second version presented in figure 67. The mean point of *Agasicles hygrophila* is the center to which the stem leads from *Disonycha argentinensis* (Da) and from which radiate the three arms, each terminating in a mean point of an *Agasicles* species as follows: vittate *A. vittata* (Av), vittate *A. interrogationis* (Ai), and fasciate lower Amazon River form of *A. opaca* (Aoa).

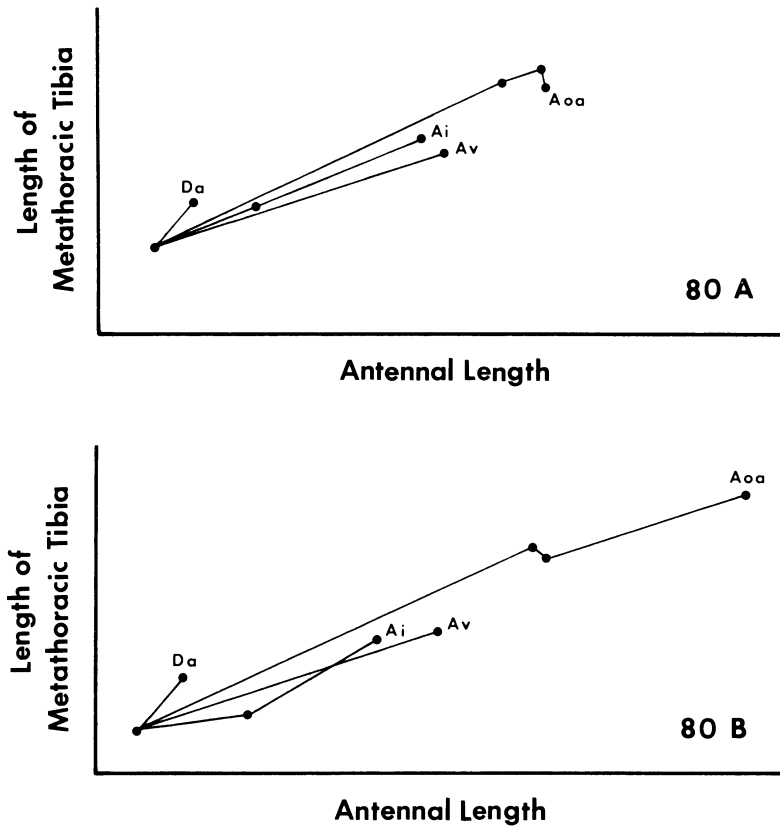


FIGURE 80.—Trifurcate (third-version) phenocline for the mean points of antennal length to metathoracic tibial length of flea beetles. A, Females. B, Males. This phenocline is at the same scale as that of the second version presented in figure 68. The mean point of *Agasicles hygrophila* is the center to which the stem leads from *Disonycha argentinensis* (Da) and from which radiate the three arms, each terminating in a mean point of an *Agasicles* species as follows: vittate *A. vittata* (Av), vittate *A. interrogationis* (Ai), and fasciate lower Amazon River form of *A. opaca* (Aoa).

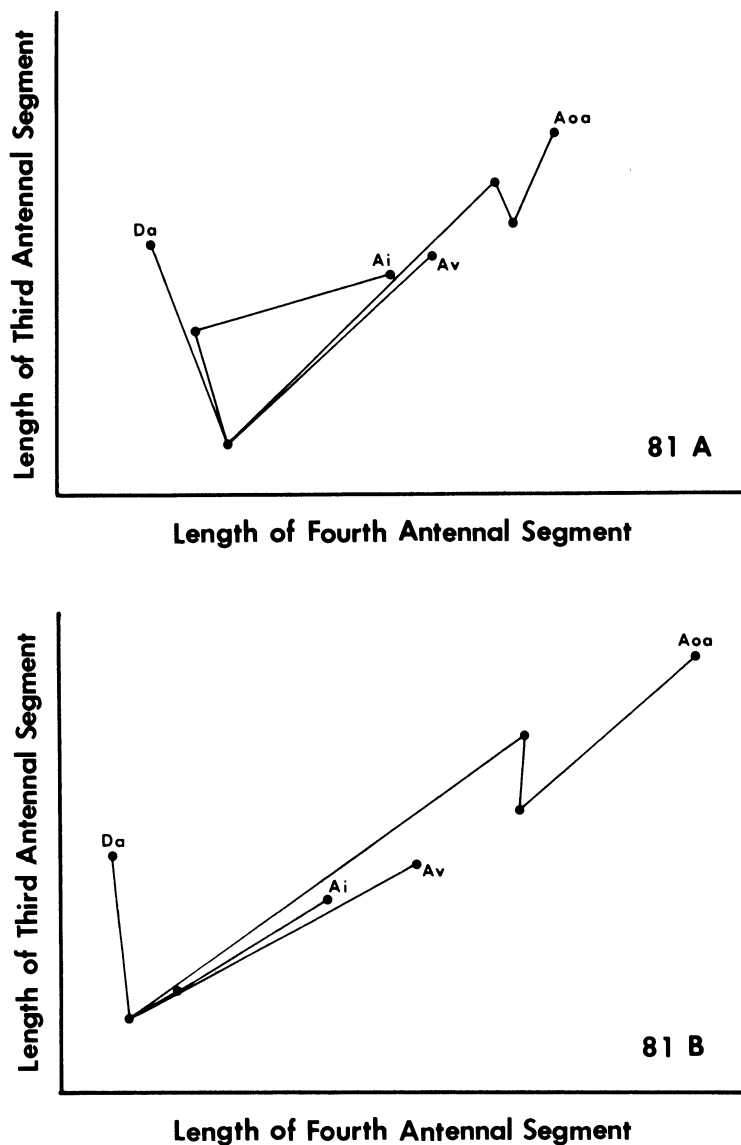


FIGURE 81.—Trifurcate (third-version) phenocline for the mean points of lengths of fourth to third antennal segments of flea beetles. A, Females. B, Males. This phenocline is at the same scale as that of the second version presented in figure 69. The mean point of *Agasicles hygrophila* is the center to which the stem leads from *Disonycha argentinensis* (Da) and from which radiate the three arms, each terminating in a mean point of an *Agasicles* species as follows: vittate *A. vittata* (Av), vittate *A. interrogationis* (Ai), and fasciate lower Amazon River form of *A. opaca* (Aoa).

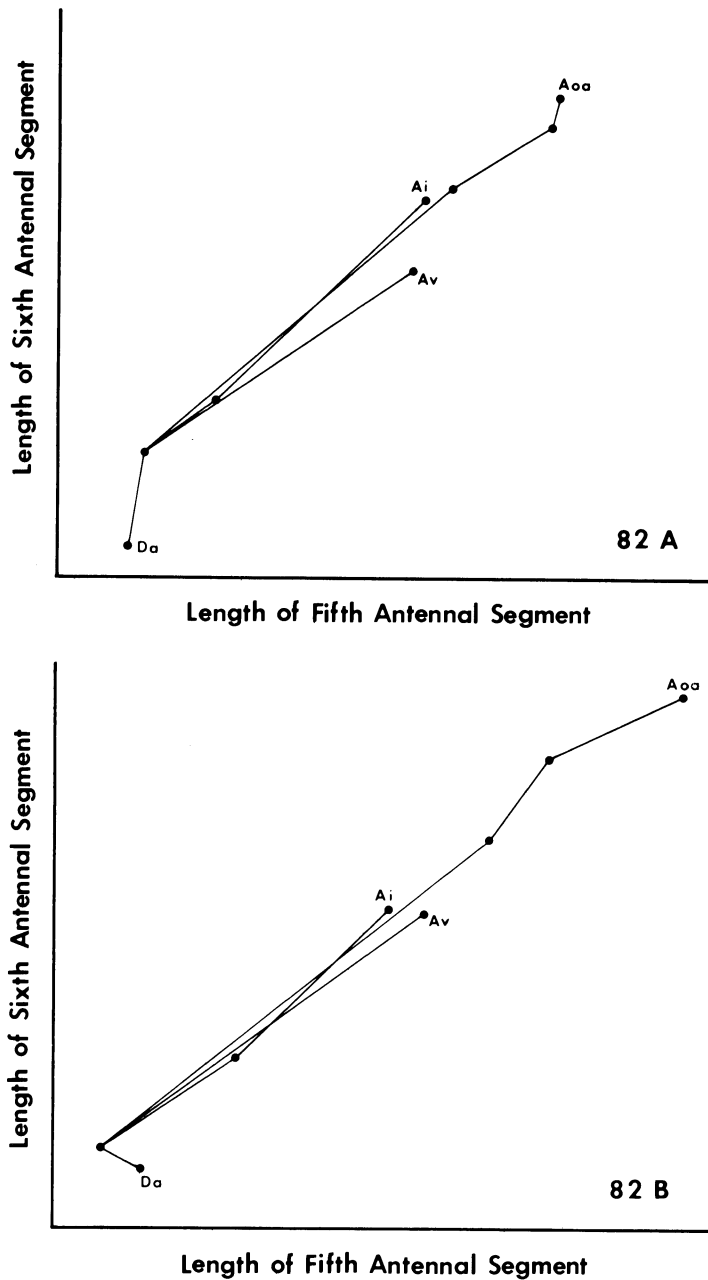


FIGURE 82.—Trifurcate (third-version) phenocline for the mean points of lengths of sixth to fifth antennal segments of flea beetles. A, Females. B, Males. This phenocline is at the same scale as that of the second version presented in figure 70. The mean point of *Agasicles hygrophila* is the center to which the stem leads from *Disonycha argentinensis* (Da) and from which radiate the three arms, each terminating in a mean point of an *Agasicles* species as follows: vittate *A. vittata* (Av), vittate *A. interrogationis* (Ai), and fasciate lower Amazon River form of *A. opaca* (Aoa).

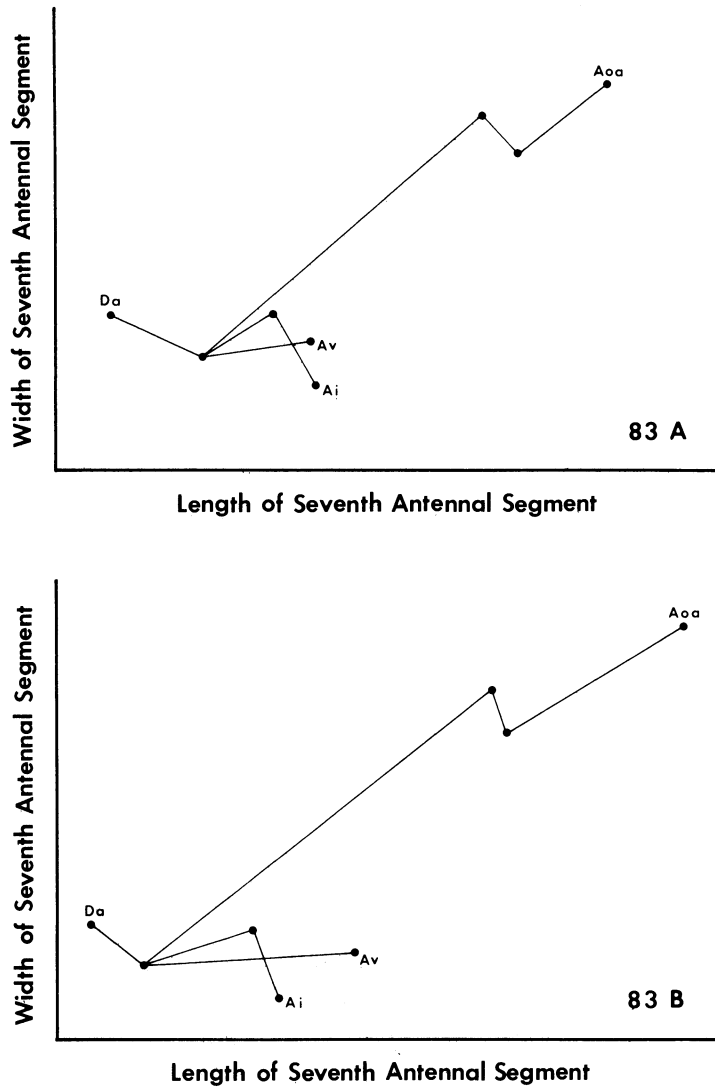


FIGURE 83.—Trifurcate (third-version) phenocline for the mean points of length to width of seventh antennal segment of flea beetles. A, Females. B, Males. This phenocline is at the same scale as that of the second version presented in figure 71. The mean point of *Agasicles hygrophila* is the center to which the stem leads from *Disonycha argentinensis* (Da) and from which radiate the three arms, each terminating in a mean point of an *Agasicles* species as follows: vittate *A. vittata* (Av), vittate *A. interrogationis* (Ai), and fasciate lower Amazon River form of *A. opaca* (Aoa).

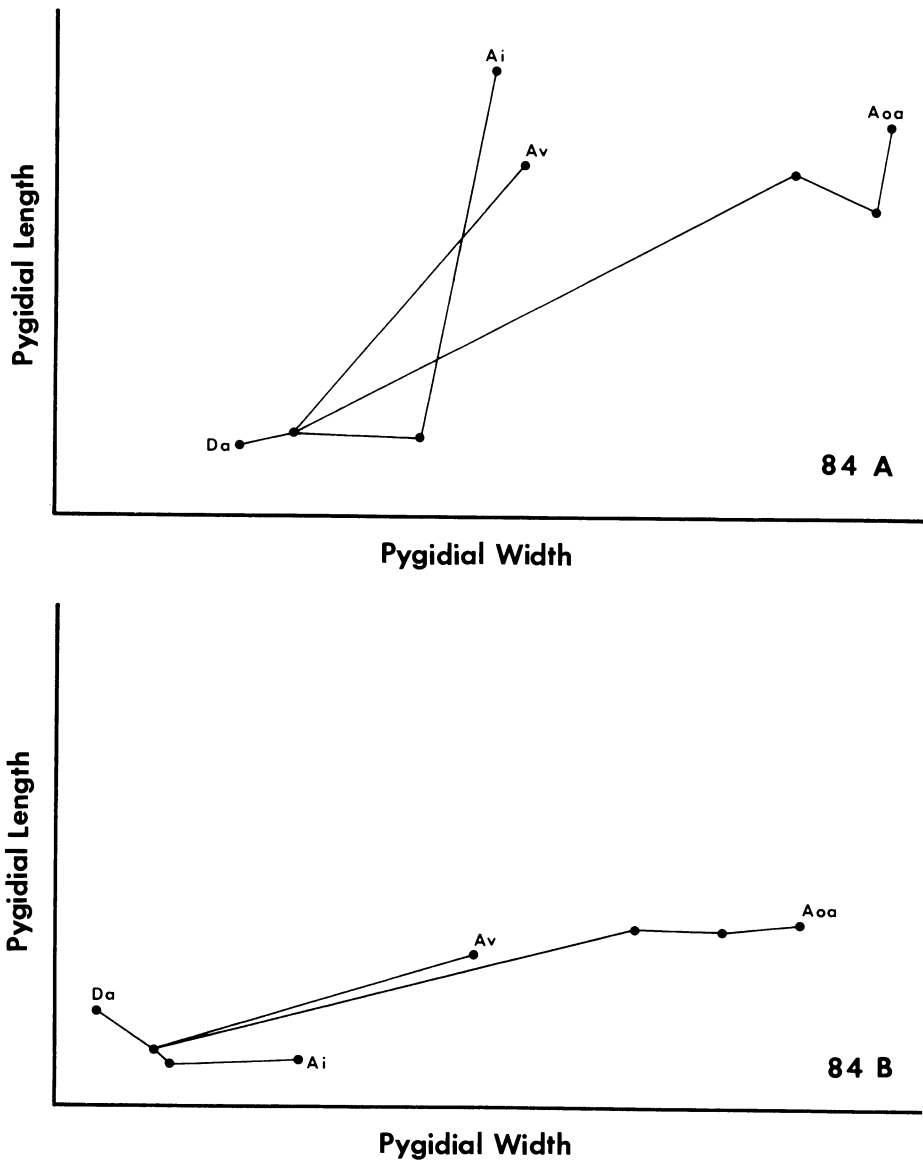


FIGURE 84.—Trifurcate (third-version) phenocline for the mean points of pygidial width to pygidial length of flea beetles. A, Females. B, Males. This phenocline is at the same scale as those of the second version presented in figure 72. The mean point of *Agasicles hygrophila* is the center to which the stem leads from *Disonycha argentinensis* (Da) and from which radiate the three arms, each terminating in a mean point of an *Agasicles* species as follows: vittate *A. vittata* (Av), vittate *A. interrogationis* (Ai), and fasciate lower Amazon River form of *A. opaca* (Aoa).

Table 13.—Total third-version phenocline distances for vittate species of *Agasicles* and for geographic forms of fasciate *A. opaca* as shown in figures 74–84, illustrating the trifurcate phenocline representation

[Millimeters]

Character pair (x to y)	Vittate <i>A. vittata</i> to <i>A. interrogationis</i>		Fasciate <i>A. opaca</i> (Paraguay River form to lower Amazon River form)		<i>A. vittata</i> to <i>A. interrogationis</i> + <i>A. opaca</i> (Paraguay River form to lower Amazon River form)	
	Total distance	Mean (n=3)	Total distance	Mean (n=2)	Total distance	Percent distance of vittate <i>Agasicles</i>
FEMALES						
PrW to PrL (fig. 74)	96	32	33	17	129	74
EL to EW (fig. 75)	85	28	38	19	123	69
BL to BTh (fig. 76)	72	24	50	25	122	59
HW to HL (fig. 77)	44	15	20	10	64	69
IOW to IAW (fig. 78)	60	20	29	15	89	67
U2W to U1W (fig. 79)	208	69	60	30	268	78
AL to MTL (fig. 80)	128	43	11	6	139	92
4AL to 3AL (fig. 81)	131	44	30	15	161	81
6AL to 5AL (fig. 82)	163	54	33	16	196	83
7AL to 7AW (fig. 83)	70	23	41	21	111	63
PyW to PyL (fig. 84)	185	62	44	22	229	81
Total	1,242	414	390	196	—	—
Percent	75	68	25	32	—	—
MALES						
PrW to PrL (fig. 74)	145	48	61	31	206	70
EL to EW (fig. 75)	95	32	45	23	140	68
BL to BTh (fig. 76)	61	21	32	16	93	66
HW to HL (fig. 77)	30	10	23	12	53	57
IOW to IAW (fig. 78)	41	14	38	19	79	52
U2W to U1W (fig. 79)	214	71	43	22	257	83
AL to MTL (fig. 80)	124	41	49	25	173	72
4AL to 3AL (fig. 81)	121	40	68	34	189	64
6AL to 5AL (fig. 82)	181	60	58	29	239	76
7AL to 7AW (fig. 83)	96	32	62	31	158	61
PyW to PyL (fig. 84)	104	35	34	17	138	75
Total	1,212	404	513	259	—	—
Percent	69	60	31	40	—	—

so much longer in the case of the vittates, with values of 68 percent for females and 60 percent for males. However, these results show clearly that the mean intermean point distances of the vittate species average greater for both females and males. For each character pair, we also present in table 13 the percentage of the total *Agasicles* phenocline taken up by the vittate species. The percentages range from 63 to 92 for the females and from 52 to 83 for the males. These results show that the total phenoclines of the vittates are longer than those of the fasciate forms for all character pairs. However, percentages based on the means of the intermean point distances show that the vittates extend less than 50 percent of the distance along the *Agasicles* phenocline for a single character pair, BL to BTh (49 percent), in the females and two character pairs, HW to HL (45 percent) and IOW to IAW (42 percent), in the males. These results show that both the total phenoclinical distances and the intermean point distances of the vittate species are greater than those of the fasciate forms for almost all character pairs for both females and males. In the third-version phenoclines as compared with those of the second version (p. 100), the lead of the vittates increases over the fasciates in the distance each takes up along the *Agasicles* phenocline. We consider this increase in the distances of the vittates as indicating a truer representation of the evolutionary history of *Agasicles*.

These third-version phenoclines more than the second versions complement the normal bivariate

ellipses in showing that there has been less divergence among the fasciate forms than among the vittate *Agasicles* forms. This evidence substantiates our view that the three fasciate *Agasicles* forms are subspecific forms of a polytypic species rather than semispecies of a superspecies as in the vittate *Agasicles* species. With these taxonomic concepts, we may make the following interpretations: Having undergone most of its evolution interacting with small-stemmed alligatorweed (and its ancestral forms), fasciate polytypic *Agasicles opaca* diverged from the vittate forms, continuing its evolution interacting mostly with oversized stems of *Alternanthera hassleriana*. While this release from the interaction with small stems relates to an accelerated rate of divergence from the vittate forms, it also relates to slowed evolution of reproductive isolation and therefore speciation among the fasciate forms. Conversely, if the speciation rate is greater with more intensive host-plant-stem and flea-beetle interaction, we may conclude that progress of the taxon cycle depends primarily upon coevolutionary processes in *Agasicles*. In such instances, counterevolutionary and coevolutionary processes could be, at least in part, one and the same. However, the evidence of our study indicates that the host plant, *Alternanthera hassleriana*, was advanced in its evolution when *Agasicles* appeared and may have changed very little structurally as the *Agasicles* species diverged and speciated geographically without resort to resource partitioning.

SUMMARY AND CONCLUSIONS

The interaction between host-plant stem and *Agasicles* pupation is unique among the Chrysomelidae. The specialized compartmentalized hollow stem of the amphibious amaranths may also be unique among both aquatic and terrestrial plants. In *Agasicles*, many marked structural modifications have resulted from the interaction which are remindful of ecological-morphological relationships existing in the stem-boring Buprestidae and Cerambycidae (Hespenheide 1969). However, the paired T-shaped "cremaster" of the pupa is unique, and the remarkable sexually dimorphic external genitalia seem to have arisen de novo and been important directly in the differentiation within the genus. Apparently indirectly, interaction with the host-plant stem has been instrumental in the speciation of *Agasicles*. However, there is no evidence that any of the forms of *Agasicles* has speciated by resource partitioning, that is, by dividing up the habitat in the form of a common host plant. This lack of habitat subdivision accounts for the allopatry and parapatry within *Agasicles* that have resulted in marked reduction in range and therefore advancement along the taxon cycle. No speciation is apparent in the other recognized specialized biotic agents of amphibious amaranths, which, like *Agasicles*, have geographic ranges that are nearly coextensive with that of alligatorweed in South America. These include *Vogtia malloi* and *Amynothrips andersoni*, both of monotypic genera, and the leaf-mining *Agromyza alternantherae* and *Disonycha argentinensis*, both of large polytypic genera. We reiterate that in *D. argentinensis* there is no interaction of host-plant stem and flea beetle.

We have considered in detail four vittate species and three subspecific fasciate forms of *Agasicles* and the close extrageneric relative, *Disonycha argentinensis*. For these South American disonychine flea beetles, we have presented three different versions of the phenoclines for 11 sets of character pairs. The first version extends through mean points of the four vittate species of *Agasicles*

and their normal ellipses to the single mean point and ellipse of the combined samples of fasciate *A. opaca*. The stem of the unbranched phenocline extends from the mean point and normal ellipse for *Disonycha argentinensis*. The second-version phenocline is essentially the same as the first version except that calibration errors are corrected and the samples of the fasciate polytypic *A. opaca* are divided into three geographical components, with the result that a series of three mean points and their normal ellipses replace the single mean point and ellipse of the first version. In the third version, the mean points are reordered, and the phenocline assumes a trifurcate form that corresponds to the trifurcate distribution of the seven forms of *Agasicles* in nature. The stem, as in the first and second versions, extends from the mean point of *Disonycha argentinensis*. Additionally, we have considered the three normal host plants of *Agasicles* in South America, namely, alligatorweed, *Alternanthera hassleriana*, and *A. sessilis*.

The stem diameters of *Alternanthera sessilis* tend to be undersized for pupating *Agasicles*, while those of alligatorweed tend to be slightly oversized. Those of *Alternanthera hassleriana* are markedly oversized. The large size of the fasciate *Agasicles* species is clearly related to the large stem size of its host plant. The somewhat smaller size of the Paraguay River form of fasciate *A. opaca* may be related to a partial dependence mostly in transition zones upon the smaller stemmed host, alligatorweed. The overall small size of the vittate species of *Agasicles* is related to the smaller stem size of their host plants, alligatorweed and *Alternanthera sessilis*. However, we have no evidence that the progression in size in the vittate species from *Agasicles hygrophila* to *A. interrogationis* and from *A. hygrophila* to *A. vittata* is related to stem diameters. Contrary to Bergman's rule, there may be instead a meaningful relationship both in vittate and fasciate *Agasicles* species of increasing insect size with increasing tropical climate and increas-

ing period since divergence from the ancestral form(s) of *A. hygrophila*, the smallest species. Later (p. 126), we will consider another possible explanation for the small size of *A. hygrophila*.

With respect to mean points for character pairs, the phenoclines show that, of the seven forms of *Agasicles*, *A. hygrophila* falls closest on the average to amphibious-amaranth-oriented *Disonycha argentinensis*. These results are consistent with zoogeographical, morphological, and biological considerations and indicate the probable extrageneric relationship between *D. argentinensis* and *A. hygrophila*. However, without the important background information, much of this proximity might be considered simply as coincidence resulting from similarity of body and appendage size. Host-plant and biogeographical information further indicates affinities among *Disonycha argentinensis*, *D. collata*, *D. xanthomelas*, and *D. glabrata*. Important in establishing relationship may be the transference of North American *D. collata* and *D. xanthomelas* to alligatorweed, a disjunct host plant for these flea beetles. Also important may be the adult-limited, disjunct orientation to alligatorweed of Western-Hemisphere-wide *D. glabrata*, observed and tested in North America but to date not found to exist in South America.

The more slender-stemmed *Alternanthera sessilis* does not occur within the range of small-sized *Agasicles hygrophila*. But this plant is an alternative host of *Agasicles connexa* and *A. interrogationis* along the east coast of Brazil. It is probable that this plant invaded the range of both of these flea beetles after each had undergone its evolution on alligatorweed. Also, *Alternanthera sessilis* supports the intermediate-sized *Agasicles vittata* exclusively over part of the flea beetle's range. This insect probably reached this acceptable host plant by coincidence after having undergone most of its evolution on alligatorweed and its ancestral forms. In the rain forest conditions of the sub-Andean ranges and possibly along the east coast of Brazil, occurrence of this host plant must be widely separated because of its dependence on tree falls for openings in the canopy. This sparse distribution of host plant may tax the searching ability of the dependent insect. Thereby, development of plants of full size may be allowed before arrival of the suppressive insect. (However, see p. 13.)

From the normal ellipses we see the conspicuously inflated internodes of decumbent stems of *Alternanthera hassleriana*, the more or less slender ascending stems of alligatorweed, and the slen-

der ascending stems of *A. sessilis*. We also see stem-diameter reduction of alligatorweed in the form of regeneration in an area denuded by *Agasicles*. Additionally, we see the length of the ascending portion of the stem related to its basal width.

Our field observations show that the forms of *Agasicles* occur allopatrically to parapatrically, or rather broadly sympatrically in the case of the Paraguay River form of fasciate *A. opaca* and vittate *A. hygrophila*. Also, as we found them occurring in the field, we show the four vittate species as a group interacting with alligatorweed as well as *Agasicles vittata* interacting alone, over part of its range, with *Alternanthera sessilis*. Similarly, we show the fasciate *Agasicles* species interacting with *Alternanthera hassleriana*. In each case, we show flea beetle size interacting with host-plant stem diameter. But because of the limitations of our sampling, we have not related each species of *Agasicles* with its particular host within the limits of its particular geographic range.

Of the graphical representations for the flea beetle characters, pronotal width related to pronotal length most clearly shows a positive relationship with diameter of the host-plant internode in which *Agasicles* pupation occurs. In contrast, pupation of most other flea beetles occurs in a cell formed by the prepupa in the soil, and the pronotum may be broad and short, as it is shown for *Disonycha argentinensis*. Elytral length related to elytral width and total length of body related to thickness of body show this relationship with stem diameter less clearly. Head width related to head length is more erratic in trend, and interocular width related to interantennal width is even more so. The last two sets of character pairs include widths that do not normally contact the restrictive walls of the host-plant internode. Therefore, these widths probably are quite free to diverge or converge. A slender prothorax and narrowed head result in the increased mobility of these structures that is apparently needed for in-stem feeding and exit-hole-making by the newly emerged flea beetle.

Other character pairs have phenoclines that seem to be related to the increases in general body size of the flea beetle species. Included here are the relations of antennal length to metathoracic tibial length, fourth to third antennal length, and sixth to fifth antennal length. Still another class of character pairs is represented by a single trend line, length to width of seventh antennal segment. It may indicate evolution of slightly more slender appendages in the vittate species of *Agasicles*,

followed by more robust appendages in the fasciate species that pupate in more spacious internode cavities.

Another class of character pairs expresses the variation of elytral markings. Our single example also seems to express the elongation of the apical region of the elytra by the widths of the bases of the concentric U-shaped elytral markings. This elongation may be related to the elongation and development of the female pygidium into an external genitalic "key." However, there is no conspicuous discordance between the pair of phenoclines to indicate sexual dimorphism. Possibly the corresponding development of the "key" in the female and the "lock" in the male cancels out much of the discordance between the sexes in the elytral apices and their associated markings.

The phenoclines are strikingly discordant between the females and the males for the relation of width to length of pygidium. This discordance is clearly a result of sexual dimorphism and reflects the development of the external genitalic key in the females, in contrast with the miniscule development of this structure in the male. With all the diversity of the 11 sets of evolutionary trend lines presented in this study, there is general concordance between the sexes except for this obviously dimorphic pair. A corresponding pair based on the development of the external genitalic lock in the male contrasted with the female was not possible because of the absence of corresponding landmarks in most females. Less obvious sexual dimorphism does occur in various character pairs. We consider that female percentages of the combined female and male distances between each of the second-version phenoclinical mean points indicate sexual dimorphism at one to three separate intervals for each of seven character pairs besides the one relating width to length of pygidium.

In most graphs of correlation between flea beetle characteristics, there is maximal intercharacter correlation because there is consistent alinement of the normal ellipses, with only a very occasional ellipse showing significant rotation from the norm. Both the vittates and fasciates show this tendency. For a few pairs of characters, however, there is diverse orientation of the ellipses; and, in such cases, there is usually a reduction in the amount of overlapping, especially if there is a sufficient interval between the mean points along the phenocline. In these there is low intercharacter correlation, a high level of discrimination, and, therefore, utility as taxonomic characters. Most notable among them

are the relations between the widths of the bases of the concentric U-shaped elytral markings and between the width and length of pygidium.

By means of the bivariate normal ellipses, diagnostic taxonomic discrimination is demonstrated for *Agasicles hygrophila* (fig. 55) and for the combined forms of *A. opaca* (figs. 50, 51, 53–55). Partial taxonomic discrimination is demonstrated for *A. interrogationis* females and *A. vittata* females (fig. 60A). Except for the character pronotal length to width (fig. 50), the normal ellipses for *Disonycha argentinensis* are either superimposed upon or else widely overlap those of the vittate species of *Agasicles*. As compared with the vittates, none of the three fasciate forms are separated by means of the normal ellipses, even though their intermean point intervals change direction markedly. Usually, it is small intermean point distance and broad, large ellipses that decrease taxonomic discrimination. Along the second-version phenoclines the totals of distances of the fasciates are less than most of those of the vittates. The differences are even greater along the third-version phenoclines. On the basis of the differentiation of their external lock-and-key genitalia, of their uncleared aedeagi, and of their elytral markings, we consider the four forms of vittate *Agasicles* as probably reproductively isolated. Since these forms are geographically exclusive and are so similar ecologically, we further consider them as being semispecies of a superspecies (Amadon 1966; MacArthur 1972; Haffer 1974). On the other hand, we have not been able to sort the three forms of fasciate *Agasicles opaca* on the basis of uncleared aedeagi, external lock-and-key genitalia, or meaningful discrimination by normal ellipses. In view of these facts and the phenoclinical distances being generally shorter in the fasciates as compared with the vittates, we consider the three fasciate *Agasicles* forms as being subspecific forms of polytypic *A. opaca* (Mayr 1970).

Although the unbranched first- and second-version phenoclines provide a consistent successive order for the mean points of the character pairs, they provide only limited evidence of the evolutionarily significant geographical separation between *Agasicles vittata* and *A. interrogationis*. The switchback in direction that occurs in a few of the phenoclines between the mean points for these two species may be important evidence if viewed from the standpoint of possible parallel evolution. But the importance is open to question because of similar switchbacks occurring along the same phenoclines between geographically proximate Paraguay



FIGURE 85.—Recent distribution of rain forests (crosshatched) and open landscapes (blank) in the Neotropics. (From Müller 1973, reprinted by permission of Dr. W. Junk b.v. Publishers.)

River and Plains of Mojós forms of fasciate *Agasicles opaca*. However, the limited evidence bearing on whether *A. vittata* has closer affinities with *A. hygrophila* or with *A. interrogationis* is consistent with extensive biogeographical evidence for a wide void between the ranges of *A. vittata* and *A. interrogationis*. Therefore, we consider that the Recent *Agasicles* species do not constitute an unbranched line or a closed circle of closely related forms but rather a trifurcate series (fig. 73). We have applied this concept in reordering the mean points for the third-version phenoclines of the 11 sets of character proportions. In this third version, the lead of the vittates increases over the fasciata for the distance each takes up along the *Agasicles* phenocline. This greater phenoclinical distance indicates more advanced speciation within the vittates

as compared within the fasciata. Biogeographical evidence supporting the trifurcate form of the phenocline follows.

Six of the seven forms of *Agasicles* are known to infest alligatorweed, and the four vittate species are known to depend either principally or exclusively upon this single host plant within their native ranges. These four species seem to be equally specialized geographic forms suppressing the same species of host plant. One of them, *Agasicles hygrophila*, is the most primitive structurally, and we consider it the least geographically derived; i.e., the most primitive member of this genus occurs either within or adjacent to the region of longest history of habitation. The other three are the more structurally and geographically derived *A. connexa* and *A. interrogationis* of the Brazilian east

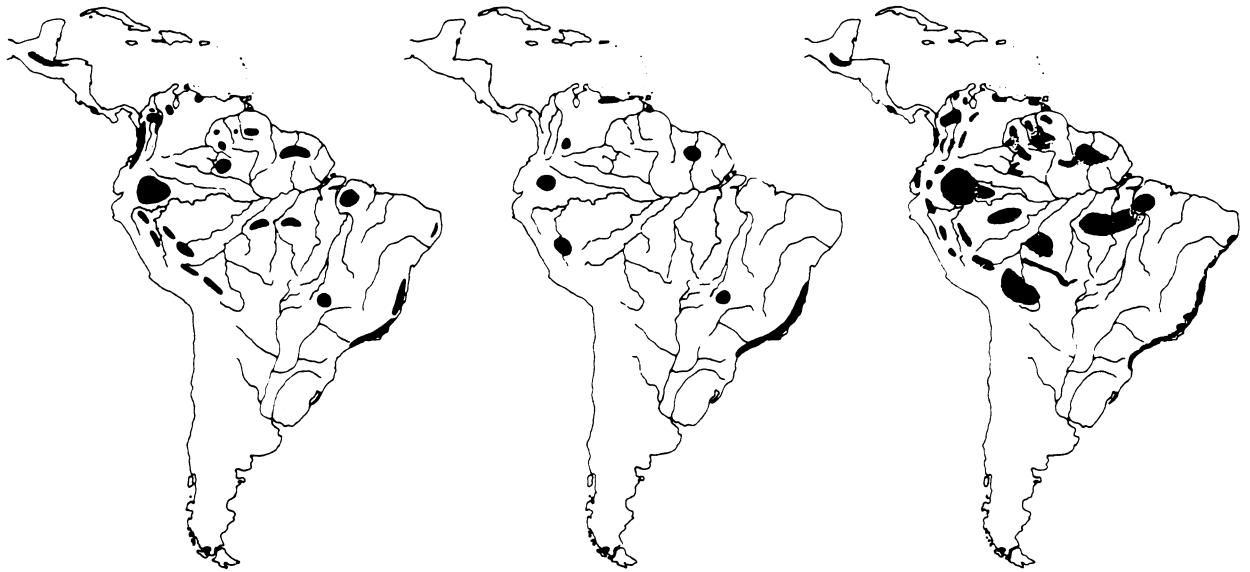


FIGURE 86.—Distribution of presumed forest refugia in the Neotropics during dry climatic phases of the Pleistocene, based upon Recent occurrences of three diverse animal groups. *Left*, neotropical bird distributions (Haffer 1974). *Center*, Amazonian lizards, *Anolis chrysolepis* species group, distributions (Vanzolini and Williams 1970). *Right*, *Heliconius* butterfly distributions (Brown et al. 1974). (From Haffer 1974, reprinted by permission of the Nuttall Ornithological Club.)

coast, and, in another direction, *A. vittata*. *Alternanthera sessilis* occurs in the range of each of the three species and is an occasional to exclusive host plant.

Except for those endemic to the region, many plant and animal species of the Atlantic coastal forest (the east Brazilian forest shown in fig. 85) have their closest relatives in the Amazonian rain forest (Smith 1962; Müller 1973; Haffer 1974). In comparing figures 34 and 85, we find this similarity very unlikely in the case of *Agasicles connexa* and *A. interrogationis*, which we judge to be more closely related to *A. hygrophila* of the lower basin of the Río de la Plata. From figures 1–6 and the phenoclines, vittate *Agasicles vittata* of the upper Amazonian forest region and fasciate *A. opaca* of the lower Amazon Basin are by the principle of parsimony clearly more distantly related than *A. hygrophila* is to the two Atlantic coastal forms of *Agasicles*. For possible comparison with these biogeographical relationships in *Agasicles*, we note the invasions of vertebrate species of the Uruguayan dispersal center (fig. 86) into the Atlantic forest of southeast Brazil as reported by Müller (1973). We also note Smith's (1962) representations of the migration of plants from the Paraguayan forest areas. To reach the Atlantic coastal forests, these plants cross over the Mesozoic basaltic shield, which we have found to be mostly a void in the

distribution of alligatorweed but apparently not in the case of the amphibious amaranth *Alternanthera reineckii*. However, we have no evidence that there was any exchange, either of forms of *Agasicles* or of forms of amphibious amaranths, across the presently unforested central tablelands separating the Amazonian forest and the forests of southeast Brazil (Smith 1962; Haffer 1974). We know of no rain-forest connections across northeastern Brazil being shown by any author. One may also consider *Agasicles* and alligatorweed as having a maritime distribution pattern along the Atlantic coast of Brazil. But as Smith (1962) points out with respect to plants, migrations have been from the north rather than from the south.

Figure 85 shows the Recent distribution of forests and open formations in South America and Central America. Figures 87 and 88 show the forested and nonforested dispersal centers as conceived by Müller (1973), and figure 86 shows the distribution of presumed forest refugia during dry climatic phases of the Pleistocene as considered by Haffer (1974). In comparing each of these distributions with those of *Agasicles* species given in figure 34, we see that *A. hygrophila*, the most primitive species, extends either along the edges of or only shallowly into three of Müller's (1973) nontorest dispersal centers, viz., the Uruguayan center (35),

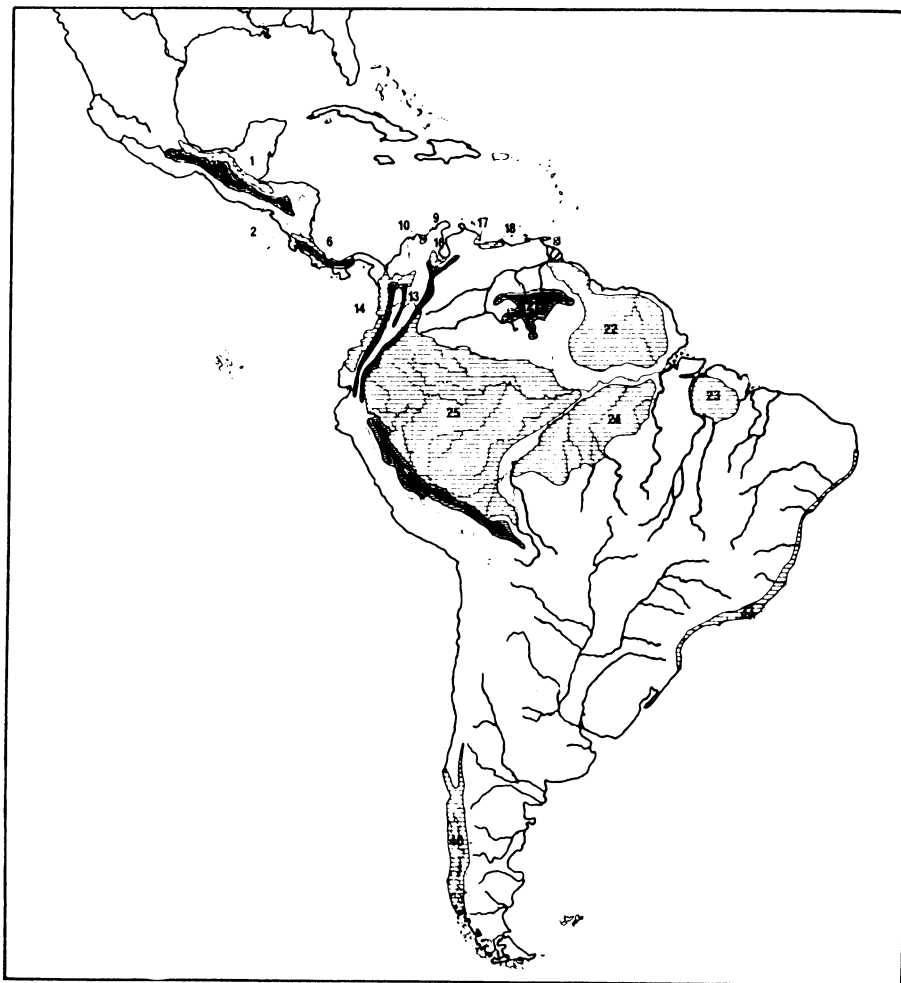


FIGURE 87.—Rain forest dispersal centers of terrestrial vertebrates in the Neotropics. Montane forest centers are shown by fine hatching and the lowland forest centers by coarse hatching. (From Müller 1973, reprinted by permission of Dr. W. Junk b.v. Publishers.)

the Pampa center (38), and the Chaco center (36).²⁶ We find further that the existing range of *Agasicles vittata* includes several rain-forest refugia con-

ceived by Müller (1973) and again, but differently, by Haffer (1974). In addition, we find that *Agasicles connexa* and *A. interrogationis* might relate to the southern subcenter and the two combined northern subcenters respectively of the Serra do Mar refugia of the Atlantic coast of Brazil (Haffer 1974). Although we do not show a map of them, Müller's (1973) Paulista subcenter and Bahia combined with the Pernambuco subcenter are even more comparable with the ranges of the two Atlantic coast *Agasicles* species.

This study shows that the unusual body form of *Agasicles* has developed largely as a result of a process of conformation to the host-plant stem in which pupation takes place. The three fasciate coccinellid-mimicking forms of *A. opaca* are more geographically derived species that developed in large stem cavities after a process of conformation

²⁶We need to point out that while these 3 dispersal centers are represented as being nonforested, gallery forest commonly occurs in them along the banks of fluvial systems. Smith (1962) refers to the complex of gallery forests of the basin of the Río de la Plata as Paraguayan rain forest. In comparison with the Amazonian rain forest, he further considers "the Paraguayan Basin [as] having developed a flora of its own to an even greater extent than has the [Atlantic] coastal rain forest." We consider the southwestern portions of the southeastern Brazilian forest shown in fig. 85 as constituting the areas of more continuous cover of the Paraguayan rain forest. We found outliers of it across Corrientes Province to the lower Paraná River. Also, we need to point out that Müller (1973) considers his Pampa center (38) to have much in common with his Uruguayan center. The endemic fauna of both centers is adapted to an unfor-
 ested landscape.



FIGURE 88.—Nonforested dispersal centers of terrestrial vertebrates in the Neotropics. *Agasicles hygrophila* and alligatorweed occur along the eastern margins of centers 36 and 38 and the western, southern, and eastern margins of center 35 (see figs. 36 and 38); *A. opaca* and *A. vittata* do not quite reach the northwest margin of region 36 (see fig. 38). (From Müller 1973, reprinted by permission of Dr. W. Junk b.v. Publishers.)

to slender stems had been achieved. All three forms have room to spare when pupating in their principal host plant, *Alternanthera hassleriana*. The oversized stem of this plant and the absence of small-stemmed regeneration that might be restrictive to *Agasicles* may constitute important evidence that the ancestral form of the Paraguay River form found the ancestral form of *Alternanthera hassleriana* with stem diameters approaching those existing today. Alternatively and possibly coevolutionarily, the flea beetle could have increased in size as the host-plant stem increased in diameter. Then, the plant stem continued to increase beyond the requirements for accommodation of the pupating insect. In the case of the vittate species of *Agasicles*, our evidence neither proves or disproves the possibility of their coevolution with

alligatorweed from exclusively terrestrial ancestral forms. Previous to this process of adaptation and speciation and possibly contemporaneous with the evolution of alligatorweed from a terrestrial to an amphibious plant, *A. hygrophila* and its precursors diverged from their ancestral form near *Disonycha argentinensis*. This step probably occurred before the Pleistocene in the basin of the Río de la Plata.

It is conceivable how the Pleistocene may well have played an important role in the speciation of *Agasicles*. Consider the very recent formation of the lower Amazonian deltaic plain. Consider the probable isolating effects of the dry climatic phases of the Pleistocene upon the Plains of Mojós and the forests of the Bolivian jungas with respect to the upper Paraguay Basin. Consider the possible isolating effects of the changes in eustatic level in the

estuarine Río de la Plata and along the eastern coast of South America. Consider the possible isolating effects of the colder climatic phases in the region of the lower Río de la Plata. Consider the effects of the dry climatic phases upon the integrity of the coastal rain forest. Then consider the present geographic ranges of the seven forms of *Agasicles*. Consider further the two probable ancestral forms of the three subspecific forms of *A. opaca*: that of the Paraguay River form of *A. opaca* and *A. hygrophila*; that of *A. vittata* and *A. hygrophila*; that of *A. hygrophila* and *A. connexa*; and that of *A. connexa* and *A. interrogationis*. The relationship within the first set of three and within each of the last two sets is especially likely, considering the close affinities within the first three and the last three existing forms and considering the similarity of their ecological niches and their adjacent geographical distributions. Consistent with this conception, Müller (1973) summarizes numerous well-documented examples of subspeciation in vertebrates that clearly took place in glacial times.²⁷

With these examples in mind it seems clear that the first changes in the differentiation of *Agasicles* probably occurred in the form of geographic variation of a wide-ranging species. There probably fol-

lowed a splitting up of the populations. In addition to the contraction and expansion of forest refugia, interglacial seas engulfing the lower Paraná River and transgressing portions of the exposed Continental Shelf of the craggy east coast of Brazil could have formed barriers and obliterated habitats for alligatorweed and its insects. During glacial advances the ancestral form near *Agasicles hygrophila* may have resorted to refugia as far north as the Pantanal and the upper Paraguay River. In this way, the flea beetle ancestral forms may have become associated with and become adapted to *Alternanthera hassleriana* or its ancestral form. Possibly climatic change, such as increasing aridity, could have separated the population of the refugium from that portion which repopulated the southern coastal regions. In this way, fasciate *Agasicles opaca* could have originated. Similarly, the ancestral forms of *Agasicles vittata* could have been cut off, as they are now, during periods of greater or less aridity, from the range of the more primitive *A. hygrophila* and its ancestral forms. The existing more primitive species, *A. hygrophila*, presently occupies a range that is central to all three branches of the dendrogram (fig. 73) which is superimposable upon the Recent pattern of geographical distribution of *Agasicles*. This trifurcate superimposability takes on added significance in view of our knowledge of dispersal capability, niche-space limits and niche-saturation capacity that characterize the component forms of *Agasicles*. In view of this background the speculations just given may be consistent with Darlington's (1970) concept that the primitive member(s) of a species complex occur more likely in the region of less stable ecology; that is, the temperate to subtropical region just south of the Tropics. However, the question remains: Has this southern region been any more climatically unstable than the Tropics which apparently alternated between wet and dry periods (Müller 1973; Haffer 1974)? On the other hand, we think it is untenable to consider the three terminal forms of the trifurcate phenocline as representing more primitive forms. It seems obvious from this study that they are the three most derived forms.

Subaquatic insects such as *Agasicles* are associated primarily with drainage systems—their alluvial plains, lagoons, and deltas. It may seem that they would be little affected by fluctuating wet to dry periods of the Pleistocene. But, in view of the dependence of the vittate species upon shade or cloud cover (low evaporation rates), and rainfall, for population increase, forest refugia may have played

²⁷Müller (1973) states: "For polytypic species with monocentric subspecies, it can be shown that the dispersal centers represent centers where terrestrial vertebrates were preserved [survived] during regressive phases of the environment; i.e., they [dispersal centers] have acted in the past as refuge areas." Even more cogent for comparison with our picture of *Agasicles* may be Haffer's (1974) conclusions: "A high percentage of neotropical birds are members of superspecies, e.g., 76% of the jacamars (Galbulidae) and 85% of the toucans (Ramphastidae). Probably, ecologic competition is an important factor in determining the range limit of numerous allied bird species in South America. I suggest that the component species of each superspecies originated from a common ancestor whose range was fragmented through vegetational changes during adverse climatic periods of the Quaternary. The 'sister' populations inhabiting the various 'refugia' deviated at differing rates from their ancestor, and from each other, by selection and chance. Upon the return of more favorable climatic and vegetational conditions newly developed forms came into secondary contact with varying results, according to which stage had been reached in the speciation process, viz., more or less extensive hybridization, geographic exclusion with no or only very limited hybridization, or range overlap of varying extent, if sexual as well as ecologic compatibility had been attained during the previous period(s) of ecologic-geographic isolation. Zones of secondary contact between Amazonian forest birds reveal striking faunal discontinuities in a continuous forest environment. Areas of faunal fusion in Middle America and Amazonia fall between postulated forest refugia and are characterized by clusters of contact zones of species and subspecies pairs."

an important role in the speciation of these forms. The present range of *Agasicles vittata* (fig. 34) coincides with Müller's (1973) and Haffer's (1974) east Peruvian presumed forest refugia (figs. 86 and 87). Likewise, the ranges of *A. connexa* and *A. interrogationis* coincide with southern and northern presumed forest refugia of the Serra do Mar. Also, in the lower Mississippi Valley region, we have found that during cold to hot-dry years introduced *Agasicles hygrophila* is unable to disperse northward from its permanent population centers along the Gulf of Mexico coast. In contrast, remarkable dispersal occurs during cool to warm-moist years (Vogt et al., cited in footnote 20).

Apparently because of their being close to the water surface on nonascending *Alternanthera hassleriana*, which has an additional feature of water-cooled stems, the fasciate forms of *Agasicles* are tolerant of insolated habitats. It may be that vittate *A. hygrophila* and possibly *A. vittata*, which should respond positively to these same features, are competitively excluded by the fasciate *Agasicles* species. Mimicry of its aposematically marked predator, *Coleomegilla quadrfasciata*, may be an important factor favoring the fasciate *Agasicles* over the vittate forms in insolated lagoons. The vittates may be more subject to predation by birds such as the widespread jaçana that characteristically range over the insolated lagoons and backwaters. In the transition zone adjacent to the habitats of *Alternanthera hassleriana*, *Agasicles hygrophila* and possibly *A. vittata* coexist on alligatorweed with the Paraguay River form and possibly the Plains of Mojós form of *A. opaca* because of better adaptation of the vittate species to alligatorweed. On the alligatorweed side of the transition zone, the larger sized fasciate *Agasicles* species are less favorably accommodated by smaller host-plant stems. Possibly, this interspecific competition has selected for small size in *Agasicles hygrophila*. None of the other vittate *Agasicles* is subject to a comparable competitive situation. Therefore, there may be greater freedom for their size increase.

The courses of the phenoclines for the vittate species of *Agasicles* suggest that a first step in the differentiation of the three species occurring along the eastern coast of South America could have been the splitting off of *A. interrogationis*, followed at a later period by the splitting off of *A. connexa*. The still more derived character of *A. vittata* indicates that it would have split off earlier from the ancestral form of *Agasicles hygrophila* than did *A. inter-*

rogationis. Alternatively, it is possible that all barriers came into existence simultaneously, and the successively increasing degrees of divergence among the vittate species of *Agasicles* could simply reflect gradients of increasing tropical climates of both Recent and earlier times. These vittate species presumably underwent their evolution principally on alligatorweed and its ancestral forms. Apparently, no intermediate forms between *Agasicles vittata* and *A. hygrophila* exist except possibly as fossils.

The somewhat different course of evolution of the three forms of fasciate *Agasicles opaca* took place on a different host plant, *Alternanthera hassleriana* and its ancestral forms. Again the phenoclines show that the geographically most remote form of *Agasicles* (lower Amazon River form) is clearly the most derived. However, prior to the appearance of the ancestral form of *Agasicles opaca*, ancestral alligatorweed probably had evolved to the more specialized *Alternanthera hassleriana* as an adaptation to the hydrographic flux of river lagoons and seasonally flooded lands such as the Plains (Llanos) of Mojós. We assume that soon after its divergence from ancestral *Agasicles hygrophila* in the upper basin of the Paraguay River the ancestral *A. opaca* increased markedly in size and invaded the Amazon Basin by way of the Plains of Mojós to become the ancestral lower Amazon River form, which continued to diverge. Presumably, the course of migration of the ancestral forms of *Agasicles vittata* followed along the forested base of the Andean foothills apart from the insolated Plains of Mojós. Like the route along the east Brazilian littoral, this route of migration is transverse to the drainage courses reaching down from the adjacent mountains (fig. 34).

Beyond its initial phases, the wide divergence between *Agasicles hygrophila* and the Paraguay River form of fasciate *A. opaca* probably occurred in situ, i.e., patristically or phyletically, with no surviving intermediate forms. In the case of the vittate species *A. vittata*, it has been supposed that one or two unknown species near its ancestral form existed in the sub-Andean region extending from southern Peru to northern Argentina. These species were considered as being intermediate in form between *A. vittata* and *A. hygrophila* (fig. 73). However, this possibility faded with the finding of *Agasicles vittata* north of Santa Cruz (Portachuelo), Bolivia, and the finding of oligophagy (stenophagy)

within *Alternanthera* of *Disonycha argentinensis* (Vogt and Cordo 1976).

Considering its subgeneric distinctness, its tropicopolitan distribution, and the rather limited geographic area where it alone is attacked by a specialized species of *Agasicles*, it may be that an important indigenous center of *Alternanthera sessilis* is in the sub-Andean region of the Amazon Basin. However, as already indicated, *Agasicles vittata* or its ancestral form probably reached this plant by coincidence in the course of its migration, after having undergone most of its evolution on *Alternanthera philoxeroides* and its ancestral forms. Over its entire worldwide range, *Alternanthera sessilis* is a slender-stemmed amphibious amaranth that, in our limited study, shows no noteworthy geographic variation. Therefore, if *A. sessilis* is indigenous to South America and if it is prehistorically tropicopolitan, it should serve to show the miniscule amount of change (coevolution) that has occurred in the host plant within those areas where it interacts with *Agasicles*. There is no evidence that the other amphibious amaranths have a prehistory of worldwide distribution. Therefore, they may not serve as indicators of coevolution. As previously cited, Pedersen considers the affinities of *A. sessilis* to be with Southeast Asian species.

Alternatively, since the primeval ecology of *Alternanthera sessilis* and *Agasicles vittata* is sylvan in the very humid sub-Andean region, the question arises, Could *Agasicles* have diverged from a terrestrial ancestral form that was a sylvan alticid in that region? There is also the possibility that the three forms of fasciate *Agasicles opaca* could have evolved independently of their vittate congeners through an ancestral form near a fasciate species of *Phenrica* (fig. 8). Neither of these alternative evolutionary courses is borne out by the findings of this study. Furthermore, the possibility that *Agasicles* underwent its radiation in a tropical region such as the basin of the Amazon River is not borne out by this study. However, in view of its lack of winter diapause coupled with its irreversible, autocidal, northward migrations documented in the lower Mississippi Valley Region (Vogt et al., cited in footnote 20), *Agasicles hygrophila* is an enigma because we consider its lack of winter hardiness as an important indicator of tropical origins. On the other hand, considering that a form of summer diapause possibly exists in *Agasicles hygrophila* (Vogt et al., cited in footnote 8) and considering that winter-diapausing flea beetles seek high ground,

we believe *Agasicles* could have lost winter hardiness as a tradeoff in evolving strong hygrophilous responses.²⁸

We interpret the findings of this study as being consistent with the center of origin and progression rule of Hennig-Brundin as discussed by Hennig (1966), Darlington (1970), Brundin (1972), Briggs (1974), and Ball (1975). Basic to this consideration are the closely comparable specializations of each of the four vittate species and each of the three fasciate forms of *Agasicles*. Additionally, there are the niche-saturation capacity, dispersal capability, and geographic exclusion characteristic of each of the forms. Our results indicate that *Agasicles hygrophila* is the most primitive species of the genus and that the genus is centered in the lower basin of the Río de la Plata. Forms extending more or less linearly in three different directions show progressively greater geographic and structural derivation (see Mayr 1970, p. 227). The trifurcate configuration of the geographical distribution and the principle of parsimony do not permit application of Darlington's rule of thumb (Darlington 1957; Nelson 1969, 1974; Brundin 1972; Ball 1975). However, in view of the closely knit character of the *Agasicles* species and the probability of their relatively recent evolution, we do not consider the applicability or nonapplicability of these rules as being important in considering this problem at this stage in geological time. Furthermore, as we have already noted (p. 120), in accordance with Amadon (1966), MacArthur (1972), and Haffer (1974), we consider that the geographically exclusive vittate species of *Agasicles* constitute four semispecies of a superspecies. They evolved primarily on alligatorweed, and they are indicated below within brackets. We also list below the three unnamed geographically exclusive fasciate *Agasicles* forms that we consider as being subspecific forms of *A. opaca* (Mayr 1970):

[<i>Agasicles connexa</i>]
	<i>interrogationis</i>	
	<i>vittata</i>	
	<i>hygrophila</i>	
<i>Agasicles opaca</i>		
Paraguay River form		
Plains of Mojos form		
Lower Amazon River form		

²⁸Lukefahr et al. (1964) point out that certain insect pests having winter diapause also have geographic ranges that do not cross the Equator. They relate this to the inability of the insects to enter diapause in areas between 10° north and 10° south latitude.

We may now recapitulate. The Recent South American disonychine flea beetles of the amphibious amaranths diverged from a terrestrial ancestral form resembling *Disonycha argentinensis* and coevolved with the amphibious amaranths. The plants were advanced in their evolution when *Agasicles* appeared. A trifurcate distribution of forms resulted that centers on *A. hygrophila*. The middle arm consists of polytypic fasciate *A. opaca*, which overlaps vittate *A. hygrophila*. The four vittate semispecies that comprise the side arms are geographically exclusive and constitute a super-species. They have evolved primarily on alligatorweed centered in the lower basin of the Río de la Plata. After having undergone most of its evolution interacting with small-stemmed alligatorweed, fasciate polytypic *A. opaca* diverged from the vittate forms, continuing its evolution interacting with mostly oversized stems of *Alternanthera hasleriana*. Although this release from interaction with small stems relates to an accelerated rate of divergence from the vittate forms, it also relates to a slowed evolution of reproductive isolation and therefore speciation among the fasciate forms.

From this summary, it becomes clear that the taxon cycle of *Agasicles* is driven to a significant degree by the plant-stem and flea-beetle interaction. This is an important consideration because, as already discussed (p. 28), Ricklefs and Cox (1972) have postulated that the progress of a species through the taxon cycle results in "counterevolution" and reduced competitive ability of that species. If this hypothesis is true, it may provide a means of recognizing promising biocontrol agents, i.e., by its stage in the taxon cycle, or, in effect, by its stage in speciation.

We need to point out further that Nelson (1974) of the emerging Croizat school of biogeographers rejects as "aprioristic all 'clues' or 'rules' used to resolve centers of origin and dispersal without reference to general patterns of vicariance²⁹ and sympatry (Croizat et al. 1974). With many others I include as a rejectable apriorism Hennig's (1966) 'Progression Rule' (Ashlock 1974). Unencumbered by aprioristic dispersal, historical biogeography is the discovery and interpretation, with reference to causal geographic factors, of the vicariance shown

by the monophyletic groups resolved by phylogenetic ('cladistic') systematics."

With respect to vicariance, we have endeavored to explain that changing geographic factors resulted in the splitting up of a wide-ranging ancestral form of *Agasicles hygrophila* into the existing seven recognized forms. Similarly we indicate the differentiation of three fasciate subspecific forms from the less wide-ranging ancestral form of *Agasicles opaca*. We feel our proposed phylogeny of *Agasicles* follows the important principles of phylogenetic systematics including Hennig's (1966) "rule of deviation" as discussed by Darlington (1970). We believe our indulgence in considerations of dispersal and center of origin are justifiably aprioristic in view of the relatively recent evolution of the existing insect forms under study and in view of our knowledge of their ecology. Furthermore, beyond the scope of this bulletin, we are assembling information (Vogt and Cordo 1976) on various interacting systems of plants and insects in South America from a biogeographical standpoint. Much of this information constitutes "tracts of distributions" that have influenced our biogeographical thinking in this bulletin.

In this study, we have laid a foundation on which more definitive studies can be made. We have presented extensive documentation on the biogeography and phylogeny of a group of specialized herbivores and their host plants that, in their interactions, provide an unusual opportunity for definitive studies. We have brought together extensive evidence for a probable center of origin of *Agasicles* in the form of *Agasicles hygrophila* and its ancestral forms. We relate evolution of the other three vittate species of *Agasicles* to three of Haffer's (1974) presumed forest refugia in tropical South America during arid climatic periods of the Pleistocene. We relate evolution of the more distinctive divergent group of three fasciate forms of *Agasicles* to three regions of open insolated wetlands to which their amphibious amaranth host is highly adapted.

We have not proved or disproved the suggested coevolution between host plant and specialized insect. We interpret our findings to mean that speciation in *Agasicles* has been a process of geographical differentiation, with the rate of speciation seemingly controlled by the intensity of the host-plant-stem and flea-beetle interaction. While this interactive process may be considered to be co-evolutionary, our findings indicate that the host plants were advanced in their evolution when *Aga-*

²⁹Vicarious species or forms, the subjects of vicariance, are important in biocontrol problems because they are ecological homologs, i.e., forms that are closely related phyletically and are essentially allopatric in distribution. They may be either semi-species of superspecies or subspecific forms of polytypic species.

sicles appeared and that the plants may not have changed appreciably as the flea beetles diverged and speciated. Our findings seem to be more in accord with the theory of sequential evolution proposed by Jermy (1976). This theory emphasizes that "the evolution of phytophagous insects follows the evolution of plants, the latter being one of the most important selection factors in the evolution of insects."

In the case of the possible coevolution of *Alternanthera hassleriana* and the three fasciate forms of *Agasicles*, the oversized host-plant stem internodes do not necessarily preclude this possibility. In the case of the possible coevolution of alligatorweed and *Agasicles hygrophila* from their terrestrial ancestral forms, the evidence remains tenuous. But if the insect ancestral forms transferred to the amphibious amaranths at a time when the plants were in an advanced state of evolution, then the plants must have either increased in growth and reproductive potential or developed phytochemical or subtle physical defenses or both, because of coevolution associated with increasing specialization, and often increasing suppressiveness, of the insects. We see little or no difference between this interactive process and that leading to ecological homeostasis that host-parasite systems evolve toward as postulated by Pimentel (1963, 1968). In phytophagous insects, the taxon cycle may be another manifestation of this same process combined with the effects of counterevolutionary processes occurring within the biotic community (see p. 28).

The piecing together of the probable evolutionary history of this group of disonychine flea beetles and their host plants affords various conclusions that are of more direct importance in the biological control of weeds. Of general interest is the evidence for and the conclusion reached on the center of origin for *Agasicles*. This information suggests the importance of the lower basin of the Río de la Plata as a center of evolution for other amphibious and aquatic weeds such as *Eichhornia*, *Pistia*, and *Sesbania* and their associated insects. Also, from the standpoint of biological control, the speciation that has taken place in *Agasicles* provides an important basis for comparison with two other important biotic agents of alligatorweed, viz., *Amynothrips andersoni* and *Vogtia malloi*. Neither of these two unrelated monotypic genera has speciated in South America, and both insects have been successfully introduced into the United States along with *Agasicles hygrophila* (Maddox et al. 1971; Brown

and Spencer 1973). The performance of these insects in the biocontrol of alligatorweed during the past few years and in the years ahead will provide important information for testing the relationship between the stages of the taxon cycle and the competitiveness of a biocontrol agent. Already monotypic *Vogtia malloi* is showing superior suppressive capability over alligatorweed under some conditions as compared with *Agasicles hygrophila* (Spencer and Coulson 1976; Vogt et al., cited in footnote 20). But monotypic *Amynothrips andersoni* may be an enigma because it is showing only limited dispersal capability (Spencer and Coulson 1976). In order that its natural dispersal capability may be further determined, we urge that no further artificial dissemination be made of *Amynothrips* beyond presently established colonies in Florida, Georgia, and South Carolina. Slow dispersal of this insect in the United States may indicate absence of a phoretic agent.

Agasicles clearly has an old, if not ancient, attachment to the amphibious amaranths that is obligatory. Its evolutionary history indicates continuation of its confinement to aquatic habitats. An insight into future evolutionary possibilities between interacting alligatorweed and *Agasicles hygrophila* within the Southern United States may be seen in this illustrated presentation of the evolutionary course that has taken place between the amphibious amaranths and *Agasicles* in South America outside the geographic range of *A. hygrophila*. No deviations from amphibious amaranths have occurred. Furthermore, in the Southern United States, no indigenous species of *Alternanthera* and no aquatic or amphibious species of plant has a stem structure that compares with alligatorweed and might serve as a suitable alternative enclosure for pupating *Agasicles hygrophila*. As compared with less specialized *Disonycha collata* and *D. xanthomelas*, *Agasicles hygrophila* and its congeners, with their many unusual specializations, may be expected to have virtually no potential for forming effective host-plant transfers (disjunctions) in the Southern United States.

We consider further the perfect transference of the North American *Disonycha collata* and *D. xanthomelas* and the imperfect orientation of *D. glabrata* to terrestrial alligatorweed in the Southern United States. Of these three North American *Disonycha* species, only *D. glabrata* reaches southern South America. This species, rather than *D. collata* or *D. xanthomelas*, may be the species most closely related to *D. argentinensis* intragenerically.

While less specialized *Disonycha xanthomelas* and *D. collata* are important suppressants of terrestrial alligatorweed in the Southern United States (Quimby and Vogt 1974), they may not prove to be as suppressive or as suppressive pangeographically as the more specialized *D. argentinensis* (pp. 23–24).

The divergence of *Agasicles* from *Disonycha* probably occurred in the wetlands associated with the Paraguay River and the Paraná River, including the vast Chaco and Pantanal. Moreover, the divergence may have required this vastness, this diversity of habitat, this geological history, because no comparable divergence in disonychines occurred in the much smaller area of wetlands in Mexico and Central America, where *Alternanthera obovata* and possibly *A. sessilis* occur indigenously and where an *Alternanthera*-oriented flea beetle quite comparable to *Disonycha argentinensis* exists indigenously in the form of *D. collata*.

Agasicles hygrophila is the smallest species of its genus, and its normal host plant, alligatorweed, is considerably larger in stem diameter than the slender-stemmed aquatic amaranth *Alternanthera sessilis*. Under normal conditions, prepupal stem entry by this flea beetle should not be hindered by the host-plant stem diameter. However, under conditions of heavy suppression by herbivores, regeneration of alligatorweed of reduced stem diameters may constitute most of the surviving plants on some sites. These reductions can be restrictive on successful metamorphosis of *Agasicles hygrophila*, because in nature, no species of *Agasicles* is known to pupate outside the host-plant stem internode. The small size of *A. hygrophila* may also simply be an expression of the restrictive effects on its evolutionary course of the reduced stem diameter cited above. This interaction may be affected by competition with the Paraguay River form of *Agasicles opaca* in the rather broad zone of overlap in their ranges. Its small size may also be simply an expression of affinity with its closest extrageneric relative, *Disonycha argentinensis*.

Biogeographical, seasonal, and ecological findings on *Agasicles* in South America are consistent with findings in North America on the progress of the introduced vittate *Agasicles hygrophila* (Maddox et al. 1971; Vogt et al., cited in footnote 20). The less insolated seasons of spring and autumn are more or less optimal for population increase. The ameliorated climate of coastal regions is also more favorable for population increase; these regions usually include the only sites of permanent popula-

tion foci as compared with the interior regions and their continental climates. Humid, cloudy, warm seasons favor population increase as compared with dry, sunny, hot seasons (Vogt et al., cited in footnote 20). Interior regions of colder latitudes may have both too brief a period of warm, cloudy, moist weather in the late spring and autumn for population increase and too severe a winter for survival of *Agasicles hygrophila*, which has no winter diapause (Maddox 1968; Vogt et al., cited in footnote 8). We doubt that this flea beetle will develop winter diapause capability or otherwise adapt itself climatically unless it is in the direction of improving its orientation to favorable environments for overwintering or for growth and development. The demonstrated dispersal capability of *Agasicles hygrophila* from its permanent population foci near the Gulf of Mexico is an important consideration for employment of this insect on other continents (Vogt et al., cited in footnote 20). Considerations of introducing *Agasicles* into tropical regions, such as Southeast Asia, should include the corresponding tropical species as well as the temperate to subtropical *A. hygrophila*.

Considering Pimentel's (1963) recommendation for avoidance of host-parasite homeostasis in biocontrol agents and considering the stage II position of the Paraguay River form of *Agasicles opaca* in the taxon cycle, this flea beetle may be useful to supplement *A. hygrophila* in suppressing alligatorweed in the United States. Also, it may be more tolerant of insolated conditions than *A. hygrophila*. However, for Pimentel's recommendations to hold, the preferred biocontrol agent may necessarily have a geographic range exclusive of that of the target weed.

With respect to the possible development of host resistance to *Agasicles hygrophila*, the normal ellipses and phenoclines may show the effect of the interaction that, in time, results in marked evolutionary change but survival of both members. This is most apparent in *Alternanthera hassleriana* versus the three fasciate *Agasicles* forms. Amelioration of this interaction seems to have occurred, resulting in greater prevalence of both plant and insect members in insolated lagoons of the Paraguay and Amazon Basins. In contrast, the interaction between alligatorweed and *Agasicles hygrophila*, which is probably the oldest involving *Agasicles*, still tends to be extirpative to the detriment of both the host plant and the dependent insect. The other vittate species of *Agasicles* are similarly extirpative.

The genus *Disonycha* ranges throughout the Western Hemisphere and is older geologically than *Agasicles*. *D. argentinensis* is somewhat apart from its congeners, apparently in the direction of *Agasicles*, with respect to certain characteristics of the adult (punctuation and form of head) and of the larva (some reduction in prominence of body tubercles and setae). The pupa, however, shows no transitional features between *Disonycha* and *Agasicles*. Also, the adult *D. argentinensis* is very distinct from its suggested closest intrageneric relative, *D. glabrata*.

In view of the terrestrial habits of *D. argentinensis*, there is probability that this insect is not confined to the terrestrial growths of aquatic amaranths, because there is on land such greater diversity of both closely and distantly related plants. However, only three terrestrial plants are known as alternative hosts. All three are species of *Alternanthera*, and it now seems unlikely that any alternative hosts exist outside this genus. None of the North American species of *Disonycha* are confined to plants of the genus *Alternanthera* except possibly *D. eximia* of the Caribbean region. None are so specialized in the direction of alligatorweed as is *D. argentinensis* of South America.

The more specialized host spectrum of *Disonycha argentinensis* indicates that it may be a more effective biocontrol agent against terrestrial alligatorweed than are the less specialized North American species, *D. xanthomelas* and *D. collata* (pp. 23–24). There is a need to determine the relative virulence or suppressive index for each of these three flea beetles in its interaction with alligatorweed. This should be done for both standardized and given simulated (special) climatic conditions. Assuming that the more specialized *D. argentinensis* is the more suppressive insect, it would have the potential to displace both *D. collata* and *D. xanthomelas* on alligatorweed, but it would have little or no effect on either North American flea beetle on their non-*Alternanthera* hosts. This problem involves ecological nonanalogs and is discussed further in Vogt and Cordo (1976). Also, assuming that the mimetic predator-ectoparasites *Lebia viridipennis*, of *Disonycha collata*, and *Lebia analis*, of *D. xanthomelas*, are sufficiently host specific not to attack *D. argentinensis*, the South American flea beetle should have an added advantage. It would be freed of its specific mimetic predator-ectoparasites, *Lebia securigera* (mimetic) and *L. concinna* (non-mimetic) (Vogt and Cordo, cited in footnote 15). With these apparent features, *Disonycha argen-*

tinensis may prove to be the ideal specialized suppressant to reduce alligatorweed along the banks of drainage canals, bayous, lagoons, and ponds. This flea beetle may show greater capability in following rooted alligatorweed behind receding waters than either *D. xanthomelas* or *D. collata*. Also, *D. argentinensis* should be important in the Gulf of Mexico region and in the Southeastern United States where *D. xanthomelas* does not occur (fig. 37) and where *D. collata* alone usually makes less impact on alligatorweed than in the region where both flea beetles occur in combination.

There can be little doubt that *Disonycha argentinensis* is a prime prospect for biocontrol of bankside alligatorweed in California, Australia, and wherever else *Alternanthera*-oriented species of *Disonycha* do not indigenously occur. The specialized host range of *D. argentinensis* should make it a safe introduction in those regions, whereas either *Disonycha xanthomelas* or *D. collata* could be destructive to various cultivated crops.

Of special interest is our proposal that introduction of one ecological homolog to compete with another for weed control may create the situation known as character displacement or ecological shift. This situation may cause division of the shared host-plant spectrum of the two homologs. The resulting reduction in number of host plants available to each homolog would constitute a process of specialization. Therefore, if more specialized phytophages are more efficient suppressants, the process could lead to improved suppression, possibly on the part of both insects. Besides division of host-plant spectrum, character displacement, or ecological shift, may occur in other ways that result in increased specialization: by division of the ecological range of the shared host plants; by division between the homologs of the anatomy of the shared host plants; and by the development of distinct periodicity on the part of the insects. If character displacement does not occur, one of the homologs may be displaced geographically, or it may become extinct. Geographical displacement may be expected to progress gradually but perceptibly within a few years. It would be associated with the development of character displacement which could be a very slow process. However, character displacement must be included in any careful consideration that is made of ecological homologs for possible introduction to control weeds.

From the grand experimental standpoint, introduction of *Disonycha argentinensis* into the South-

ern United States might show to what degree the hypothesis holds that the more specialized herbivore is the more efficient host suppressant. From another angle, such an introduction might show a relationship between degree of specialization of herbivore (consumer species) to environmental stability or homeostasis. It might help us to understand why some specialized agents such as many leaf miners are only lightly suppressive. Is it simply because of parasite-predator pressure? In this connection, but seemingly inconsistent while being seemingly cogent, are the recently proposed rating criteria for biotic agents in which Harris (1973) downgrades specialization while emphasizing how vitally the insect's attack affects the plant. Yet Frick (1974) judiciously points out that there are two criteria of primary importance in choosing candidate insects for biocontrol: "(1) a narrow range of host plants, none of which can be crop plants [a manifestation of specialization] and (2) an attack by the plant feeding stages (larvae, nymphs, adults) of growing tissues vital to the plant rather than tissues of little importance to plant growth such as senescent foliage or pith." The shift by phytophages from more vital host tissues to those that are less so is an obvious evolutionary course leading to homeostasis, and it seems to have occurred in some specialized leaf miners that have shifted in orientation from young leaves to older leaves. However, we recognize no comparable shift having occurred in any of the *Disonycha* oriented to *Alternanthera*.

We close with consideration of still another view expressed by Huffaker et al. (1971): "Theoretically, general predators tend to serve as regulators of community stability while specialists tend to regulate single species stability. . . . There is no sharp line; the two are interrelated. . . ." With this view in mind it seems clear to consider the gypsy moth, *Lymantria dispar*, as an exotic organism and as a general predator that is capable of regulating community stability in the Eastern North American forest formation. Presumably, this insect can be considered to have similar but reduced capability in its indigenous range in the Old World. Also, we may consider without semantic difficulties that both specialized *Agasicles hygrophila* and *Vogtia malloi* are capable of regulating alligatorweed, both in its indigenous ranges in South America and in the Southern United States.

This field-oriented systematic study of a biocontrol agent and related species together with their host plants is intended to complement laboratory studies employed in the screening of biocontrol agents. The field-oriented systematic approach affords contextual perspective not usually or readily obtainable in laboratory screening studies. Much of the type of information that field-oriented systematic studies are based upon is stored in biological collections, but both field studies and the biological literature are necessary for development of the context.

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APPENDIX

Analytical Data for Measured Flea Beetle and Amphibious Amaranth Characters

Table A-1.—Composition of measured samples of host plants

<i>Alternanthera</i> species and growth habit	Number of stems measured	Locality	Suppressant <i>Agasicles</i> species
<i>A. philoxeroides</i> ; regeneration of <i>Agasicles</i> - suppressed plants; leaves of each stem infested with larvae. Fig. 48, ellipse D ($n=12$).	12	Banks of Reconquista River near Caste- lar, Buenos Aires Province, Argentina.	<i>A. hygrophila</i> .
<i>A. philoxeroides</i> ; at margin of incipient mat, float- ing, possibly approaching a form with a cordlike attachment. Figs. 47 and 48, point E.	1	Laguna Espejo near Santa Fe, Sante Fe Province, Argentina.	Do.
<i>A. philoxeroides</i> ; usually competing among erect stems; collected within the known range of the vittate species of <i>Agasicles</i> . Fig. 47, ellipse C ($n=88$) and fig. 48, ellipse C ($n=92$). ¹	17	Deltaic marshland at head of the Guaíba River, Ilha do Pavão, Rio Grande do Sul State, Brazil.	Do.
Do	3	Roadside pools near San Miguel del Monte, Buenos Aires Province, Argentina.	Do.
Do	7	Deltaic swamp, Brazo Largo near Yaraví, Entre Ríos Province, Argentina.	Do.
Do	3	Deltaic marshland, Río de las Palmas near Campana, Buenos Aires Province, Argentina.	Do.
Do	1	Laguna Espejo near Santa Fe, Santa Fe Province, Argentina.	Do.
Do	5	Arroya Riachuelo near Corrientes, Cor- rientes Province, Argentina.	Do.
Do	2	Ituzaingó, Corrientes Province, Argentina	Do.
Do	1	Itá-Ibaté, Corrientes Province, Argentina	Do.
Do	2	Streetside ditches, Posadas, Misiones Pro- vince, Argentina.	Do.
Do	2	Shallow cove of Paraná River at Posadas, Misiones Province, Argentina.	Do.
Do	4	Drying lagoons along Paraguay River oppo- site Asunción, Paraguay.	Do.
Do	2	Delta (?) of Itajaí River at Itajaí, Santa Catarina State, Brazil.	<i>A. connexa</i> .
Do	4	Praia Braba, just south of Cabeçadas, Santa Catarina State, Brazil.	Do.
Do	25	Paranaguá, Paraná State, Brazil	Do.
Do	11	Dique district, Salvador, Bahia State, Brazil.	<i>A. interrogationis</i> .
Do	4	Vermelho River near Salvador, Bahia State, Brazil.	Do.
Do	7	Salvador, Bahia State, Brazil	Do.

See footnotes at end of table.

Table A-1.—Composition of measured samples of host plants—Continued

<i>Alternanthera</i> species and growth habit	Number of stems measured	Locality	Suppressant <i>Agasicles</i> species
<i>A. philoxeroides</i> ; usually competing among erect stems; collected within the known range of the vittate species of <i>Agasicles</i> . Fig. 47, ellipse C ($n=88$) and fig. 48, ellipse C ($n=92$). ¹ —Continued	11	Banks of Amazon River at Leticia, Amazonas, Colombia.	<i>A. vittata</i> .
Do	23	Iquitos, Loreto Department, Peru	Do.
<i>A. sessilis</i> ; competing among erect stems. Figs. 47 and 48, ellipse F ($n=28$).	14	Huallaga River near Tulomayo, Huánuco Department, Peru.	Do.
Do	4	Streetside ditch, Pucallpa, Loreto Department, Peru.	Do.
Do	9	Banks Amazon River at Leticia, Amazonas, Colombia.	Do.
<i>A. hassleriana</i> ; free floating but with cordlike attachment. Figs. 47 and 48, ellipse B ($n=13$).	10	Ilha Careira, Amazon River, Amazonas State, Brazil.	<i>A. opaca</i> .
Do	3	Lago Branco, Monte Alegre, Pará State, Brazil.	Do.
<i>A. hassleriana</i> ; competing among large <i>Eichhornia</i> at edge of dry lagoon (the normally floating plants from the dry lagoons are unsuitable for measurement). Figs. 47 and 48, points A.	3	Drying lagoons along Paraguay River opposite Asunción, Paraguay.	Do.

¹An inadvertent mismatch of samples of measured specimens is represented by $n=88$ and $n=92$.

²Accessioned specimens of U.S. National Herbarium.

Table A-2.—Measurement reliability for four characters of *Alternanthera philoxeroides* and *A. hassleriana* herbarium specimens¹
[Millimeters]

Character ²	Measurement date, 1972			Mean	SD	CV (%)	Measurement date, 1972			Mean	SD	CV (%)
	July 11	July 27	August 16				July 11	July 27	August 16			
<i>A. philoxeroides</i> (specimen 2138-a)												
Int'n W1	3.800	3.800	3.900	3.833	0.0577	0.02	7.000	7.000	7.000	7.000	0.000	0.00
Int'n L	41.50	42.00	42.00	41.83	.2887	.01	80.00	79.80	81.00	80.27	.6429	.01
Ascdng L	240.0	245.0	243.0	242.7	2.5166	.01	247.0	255.0	260.0	254.0	6.557	.03
Int'n W3	7.000	6.000	6.500	6.500	.5000	.08	6.800	6.700	7.300	6.933	.3215	.05
<i>A. hassleriana</i> (specimen 1231-a)												
Int'n W1	16.000	16.000	16.500	16.167	0.2887	0.18	18.000	16.000	16.000	16.667	1.1547	0.07
Int'n L	48.00	45.00	42.00	45.000	3.000	.07	46.00	46.00	45.00	45.67	.5774	.01
Ascdng L	15.000	15.000	17.000	15.83	1.0408	.07	12.00	12.00	10.00	11.333	1.1547	.10
Int'n W3	8.000	8.500	7.000	7.833	.7638	.10	5.500	6.000	6.000	5.833	.2887	.05
<i>A. hassleriana</i> (specimen 1231-b)												

¹In Vogt's herbarium. SD, Standard deviation. CV, Coefficient of variation.

²Abbreviations are identified in table 3.

Table A-3.—Composition of measured samples of flea beetles

Flea beetle	Number measured		Locality	<i>Alternanthera</i> host-plant species	Unused preserved specimens
	♀	♂			
<i>Disonycha argentinensis</i>	6	6	Fallow dry fields near Reconquista River and Castelar, Buenos Aires Province, Argentina.	<i>A. philoxeroides</i> . . .	41
<i>Agasicles hygrophila</i> (n=45 ♀, 42 ♂).	1	0	Vila Nova, Rio Grande do Sul State, Brazil	do	0
Do	2	4	Ilha do Pavão, Rio Grande do Sul State, Brazil	do	0
Do	16	16	Montevideo, Uruguay	do	102
Do	3	3	San Miguel del Monte, Buenos Aires Province, Argentina.	do	0
Do	3	0	Yaraví, Entre Ríos Province, Argentina	do	1
Do	3	4	Río de las Palmas near Campana, Buenos Aires Province, Argentina.	do	14
Do	13	14	Reconquista River near Castelar and Las Barrancas, Buenos Aires Province, Argentina.	do	205
Do	3	1	Santa Fe, Santa Fe Province, Argentina	do	0
Do	1	0	Arroya Riachuelo near Corrientes, Corrientes Province, Argentina.	do	1
<i>Agasicles connexa</i>	5	10	Itajaí, Santa Catarina State, Brazil	do	0
<i>Agasicles interrogationis</i> (n=18 ♀, 18 ♂).	5	9	Dique district, Salvador, Bahia State, Brazil	do	0
Do	13	9	Cachoeira River near Itabuna, Bahia State, Brazil.	do	5
<i>Agasicles vittata</i> (n=14 ♀, 23 ♂).	1	0	Huallaga River near Tingo María, Peru	<i>A. sessilis</i>	0
Do	0	15	Huallaga River near Tulomayo, Peru	do	0
Do	13	8	Amazon River near Leticia, Colombia	<i>A. philoxeroides</i> and <i>A. sessilis</i> .	8
<i>Agasicles opaca</i> , Paraguay and Amazon River forms combined (n=31 ♀, 28 ♂).	2	1	Shallow, pristine lagoons along Riachuelo Antiquera above Puerto Antiquera, Chaco Province, Argentina.	<i>A. hassleriana</i>	0
Do	10	11	Turbid lagoons, disturbed by cattle, near Barranqueras, Chaco Province, Argentina.	<i>A. hassleriana</i> and <i>A. philoxeroides</i> .	0
Do	1	1	Seasonally dry lagoons along Paraguay River opposite Asunción, Paraguay.	do	0
Do	12	12	Lago Careira, clear-water lagoon of Amazon flood plain below Manaus, Amazonas State, Brazil.	<i>A. hassleriana</i> , <i>A. philoxeroides</i> , and <i>A. sessilis</i> .	0
Do	6	3	Clear, pristine "varzea" lagoon of Amazon flood plain near Monte Alegre, Pará State, Brazil.	<i>A. hassleriana</i>	0

Table A-4.—Measurement reliability for 22 characters of preserved *Agasicles hygrophila* specimens¹

Character ²	Specimen Ag-45, ♀						Specimen Ag-46, ♀					
	Measurement date, 1972			Mean (mm)	SD (mm)	CV (%)	Measurement date, 1972			Mean (mm)	SD (mm)	CV (%)
	April 15	May 3	June 5				April 15	May 3	June 5			
TBL	5.500	5.500	5.500	5.500	0.000	0.0	6.100	5.500	5.700	5.767	0.306	5.3
EW	2.450	2.440	2.490	2.69	.231	1.17	2.600	2.600	2.600	2.600	.000	.0
BTh	1.800	1.890	1.850	1.847	.045	2.4	1.900	1.910	1.850	1.887	.032	1.7
HL	.468	.530	.421	.473	.055	11.6	.468	.437	.390	.432	.039	9.1
HW	.998	1.014	.998	1.004	.009	.9	.967	.970	.964	.967	.003	.3
IAW	.072	.075	.072	.073	.002	2.4	.060	.065	.061	.062	.003	4.6
IOW	.224	.211	.221	.219	.007	3.3	.209	.203	.203	.205	.004	1.7
PrL	.998	1.045	1.014	1.019	.024	2.3	.967	.936	.952	.952	.016	1.6
PrW	1.295	1.310	1.310	1.305	.009	.7	1.310	1.310	1.310	1.310	.000	.0
EL	3.950	4.000	3.900	3.950	.050	1.3	4.100	4.090	4.120	4.103	.015	.4
U2W	.577	.562	.561	.567	.009	1.6	.562	.655	.624	.614	.048	7.8
U1W	.374	.346	.374	.365	.016	4.4	.265	.265	.281	.2704	.009	3.
PyL	.296	.343	.281	.307	.033	10.6	.312	.312	.281	.302	.018	6.0
PyW	.842	.920	.858	.874	.041	4.7	.858	.905	.889	.8840	.024	2.7
MTL	1.217	1.248	1.279	1.248	.031	2.5	1.186	1.248	1.279	1.238	.048	3.9
AL	2.700	2.860	2.800	2.787	.081	2.9	2.610	2.700	2.720	2.677	.059	2.2
3AL	.084	.081	.084	.083	.002	2.1	.090	.072	.077	.0780	.009	11.6
4AL	.120	.120	.120	.120	.000	.0	.125	.111	.120	.119	.008	6.3
5AL	.102	.108	.107	.105	.003	3.1	.099	.099	.101	.100	.001	1.4
6AL	.096	.091	.096	.094	.003	2.9	.096	.091	.096	.094	.003	2.9
7AL	.090	.096	.090	.092	.004	3.8	.090	.096	.090	.092	.004	3.8
7AW	.060	.057	.053	.057	.003	5.8	.060	.056	.053	.057	.003	5.8

¹In Vogt's collection. SD, Standard deviation. CV, Coefficient of variation.²The abbreviations are identified in table 4. The measurements are illustrated in fig. 46.

Table A-5.—Means, standard deviations (SD), and coefficients of correlation (*r*) for the two pairs of characters measured in three *Alternanthera* species

[Millimeters]

Correlated characters ¹		<i>Alternanthera sessilis</i> (<i>n</i> =28)	<i>Alternanthera hassleriana</i> (<i>n</i> =13)	<i>Alternanthera philoxeroides</i> (<i>n</i> =88)	<i>Alternanthera philoxeroides</i> regeneration (<i>n</i> =12)
<i>x</i>	<i>y</i>				
Ascdng L	Int'n W3:				
Mean	<i>x</i>	197.25	18.307	326.4	—
	<i>y</i>	1.6714	5.523	4.489	—
SD	<i>x</i>	84.61	9.499	179.28	—
	<i>y</i>	.4822	2.4235	1.9842	—
<i>r</i>		.7172	.9415	.01534	—
Int'n L	Int'n W1:				
Mean	<i>x</i>	35.32	47.54	51.77	43.75
	<i>y</i>	1.4036	14.75	3.450	1.933
SD	<i>x</i>	8.577	7.590	17.66	17.499
	<i>y</i>	.2516	3.875	1.202	3.114
<i>r</i>		.3581	.2058	.1707	.5422

¹Character abbreviations are identified in table 3.

Table A-6.—Means, standard deviations (SD), and coefficients of correlation (*r*) for the 11 pairs of characters measured in females of the 6 flea beetle species

[Millimeters]

Correlated characters ¹		<i>Disonycha argentinensis</i> (<i>n</i> =6)	<i>Agasicles hygrophila</i> (<i>n</i> =45)	<i>Agasicles connexa</i> (<i>n</i> =5)	<i>Agasicles interrogationis</i> ²	<i>Agasicles vittata</i> (<i>n</i> =14)	<i>Agasicles opaca</i> (<i>n</i> =31)
<i>x</i>	<i>y</i>						
PrW	PrL:						
Mean	<i>x</i>	1.5834	1.2146	1.3291	1.2995	1.3284	1.8282
	<i>y</i>	.8112	.9276	1.0577	1.0178	1.0109	1.3421
SD	<i>x</i>	.0422	.0671	.0710	.0541	.0522	.0887
	<i>y</i>	.0197	.0504	.0356	.0337	.0386	.0744
<i>r</i>		.5615	.8297	.8964	.6907	.7959	.6243
EL	EW:						
Mean	<i>x</i>	3.9233	3.8533	4.0700	4.4072	4.3886	5.3290
	<i>y</i>	2.5383	2.2702	2.4780	2.4261	2.4143	3.4184
SD	<i>x</i>	.0852	.2444	.2225	.1537	.1747	.2735
	<i>y</i>	.0376	.1644	.1158	.0979	.1299	.2472
<i>r</i>		.7251	.6851	.8507	.6625	.8898	.5619
BL	BTh:						
Mean	<i>x</i>	5.4167	5.4109	5.7800	6.3833	6.2429	7.5968
	<i>y</i>	1.6950	1.6958	1.8000	1.7933	1.8400	2.4113
SD	<i>x</i>	.1169	.4568	.2387	.2618	.1785	.5199
	<i>y</i>	.0394	.1245	.0612	.0827	.1295	.1243
<i>r</i>		.6735	.7204	.9405	.6545	.8352	.5911
HW	HL:						
Mean	<i>x</i>	1.0389	.9441	1.0083	.9613	.9621	1.1804
	<i>y</i>	.5096	.4536	.4867	.4437	.4829	.5973
SD	<i>x</i>	.0273	.0411	.0206	.0245	.0287	.0525
	<i>y</i>	.0426	.0341	.0171	.0279	.0342	.0449
<i>r</i>		.4857	.5699	-.3176	-.0581	.5611	.1857

See footnotes at end of table.

Table A-6.—Means, standard deviations (SD), and coefficients of correlation (*r*) for the 11 pairs of characters measured in females of the 6 flea beetle species—Continued

[Millimeters]

Correlated characters ¹		<i>Disonycha argentinensis</i> (<i>n</i> =6)	<i>Agasicles hygrophila</i> (<i>n</i> =45)	<i>Agasicles connexa</i> (<i>n</i> =5)	<i>Agasicles interrogationis</i> ²	<i>Agasicles vittata</i> (<i>n</i> =14)	<i>Agasicles opaca</i> (<i>n</i> =31)
<i>x</i>	<i>y</i>						
IOW	I AW:						
Mean <i>x</i>	.2397	.2068	.2129	.1963	.2001	.2716
 <i>y</i>	.0847	.0677	.0568	.0647	.0718	.0944
SD <i>x</i>	.0117	.0100	.0053	.0075	.0077	.0126
 <i>y</i>	.0070	.0046	.0024	.0050	.0051	.0062
<i>r</i>9092	.4128	.6988	.3057	.5220	.5808
U2W	U1W:						
Mean <i>x</i>	.3562	.3596	.6259	.7448	.5837	1.0678
 <i>y</i>	.4732	.4618	.2952	.2378	.2458	.3306
SD <i>x</i>	.0428	.0816	.0403	.0490	.0336	.0930
 <i>y</i>	.0780	.0833	.0679	.0542	.0435	.1017
<i>r</i>	-.8866	-.3415	.2947	-.4279	-.2531	-.3395
AL	MTL:						
Mean <i>x</i>	2.6450	2.5860	2.7700	3.1328	3.1779	3.3852
 <i>y</i>	1.2064	1.1252	1.2199	1.3676	1.3583	1.5323
SD <i>x</i>	.0464	.1428	.1483	.1419	.1057	.2052
 <i>y</i>	.0470	.0677	.0473	.0579	.0881	.1029
<i>r</i>5157	.7910	.8502	.5046	.7345	.6586
4AL	3AL:						
Mean <i>x</i>	.1037	.1120	.1093	.1334	.1375	.1517
 <i>y</i>	.0922	.0736	.0825	.0894	.0923	.1050
SD <i>x</i>	.0065	.0094	.0149	.0094	.0091	.0122
 <i>y</i>	.0055	.0079	.0130	.0075	.0072	.0084
<i>r</i>	-.0672	.5231	-.1724	.5220	.4826	.5004
6AL	5AL:						
Mean <i>x</i>	.0937	.0963	.1017	.1216	.1205	.1314
 <i>y</i>	.0807	.0900	.0957	.1141	.1081	.1219
SD <i>x</i>	.0031	.0074	.0042	.0058	.0078	.0119
 <i>y</i>	.0050	.0064	.0060	.0051	.0076	.0079
<i>r</i>4629	.5812	.7071	.3949	.8398	.6207
7AL	7AW:						
Mean <i>x</i>	.0877	.0944	.1041	.1088	.1081	.1345
 <i>y</i>	.0592	.0551	.0592	.0520	.0565	.0840
SD <i>x</i>	.0072	.0069	.0033	.0036	.0079	.0116
 <i>y</i>	.0010	.0046	.0071	.0034	.0049	.0096
<i>r</i>1974	.6634	-.3059	.4849	-.1688	.5875
PYW	PYL:						
Mean <i>x</i>	.7800	.8033	.8611	.8958	.9101	1.0482
 <i>y</i>	.2600	.2718	.2683	.6130	.5215	.4932
SD <i>x</i>	.0261	.0508	.0131	.0328	.3423	.0554
 <i>y</i>	.0189	.0541	.0171	.0570	.0697	.0694
<i>r</i>	-.6908	.2698	-.8729	-.0546	.1847	.0555

¹Character abbreviations are identified in table 4. The measurements are illustrated in fig. 46.

²*n* = 18 except for the PYW-PYL correlation, where *n* = 17.

Table A-7.—Means, standard deviations (SD), and coefficients of correlation (*r*) for the 11 pairs of characters measured in males of the 6 flea beetle species

[Millimeters]

Correlated characters ¹		<i>Disonycha argentinensis</i> (<i>n</i> =6)	<i>Agasicles hygrophila</i> (<i>n</i> =42)	<i>Agasicles connexa</i> (<i>n</i> =10)	<i>Agasicles interrogationis</i> (<i>n</i> =18)	<i>Agasicles vittata</i> (<i>n</i> =23)	<i>Agasicles opaca</i> (<i>n</i> =28)
<i>x</i>	<i>y</i>						
PrW	PrL:						
Mean <i>x</i>	1.435	1.107	1.222	1.187	1.208	1.699
 <i>y</i>	.805	.8588	.955	.949	.955	1.289
SD <i>x</i>	.0843	.0635	.0545	.0548	.0500	.0868
 <i>y</i>	.0434	.0621	.0464	.0338	.0382	.0930
<i>r</i>9506	.6598	.8541	.7390	.8614	.8202
EL	EW:						
Mean <i>x</i>	3.580	3.440	3.540	4.054	4.0500	4.982
 <i>y</i>	2.180	1.941	2.085	2.133	2.1621	3.020
SD <i>x</i>	.2445	.1730	.4326	.2922	.2505	.4137
 <i>y</i>	.1195	.1192	.1029	.1129	.1064	.2145
<i>r</i>9312	.8359	.8514	.5566	.8646	.8101
BL	BTh:						
Mean <i>x</i>	4.977	4.831	5.040	5.444	5.487	6.736
 <i>y</i>	1.483	1.456	1.545	1.612	1.643	2.182
SD <i>x</i>	.3871	.2781	.3026	.1977	.3152	.4388
 <i>y</i>	.0880	.0731	.1165	.1229	.0806	.1588
<i>r</i>9460	.7247	.9043	.3720	.8014	.6676
HW	HL:						
Mean <i>x</i>	.9558	.8861	4.054	.911	.915	1.123
 <i>y</i>	.4477	.4141	2.133	.4378	.4415	.5583
SD <i>x</i>	.0549	.0317	.2922	.0224	.0303	.0523
 <i>y</i>	.0464	.0251	.1129	.0468	.0327	.0460
<i>r</i>9692	.5111	.5566	.2395	.2807	.5152
IOW	IAW:						
Mean <i>x</i>	.2113	.1892	.1904	.1770	.1872	.2614
 <i>y</i>	.0757	.0603	.0518	.0571	.0624	.0861
SD <i>x</i>	.0145	.0085	.0087	.0093	.0080	.0160
 <i>y</i>	.0106	.0059	.0030	.0053	.0059	.0065
<i>r</i>9126	.6220	.6507	.3282	.3131	.7336
U2W	U1W:						
Mean <i>x</i>	.3406	.2960	.5713	.662	.5209	.977
 <i>y</i>	.4472	.4517	.2761	.2349	.2225	.2997
SD <i>x</i>	.0553	.0628	.0587	.0555	.0409	.0697
 <i>y</i>	.0824	.0902	.0706	.0542	.0377	.0610
<i>r</i>0392	-.7231	-.6291	-.6475	-.0097	-.0311
AL	MTL:						
Mean <i>x</i>	2.628	2.535	2.768	3.047	3.179	3.666
 <i>y</i>	1.164	1.042	1.0811	1.247	1.266	1.553
SD <i>x</i>	.1207	.1544	.1847	.1088	.1287	.2681
 <i>y</i>	.0482	.0626	.0560	.0667	.0814	.1000
<i>r</i>9826	.6834	.9471	.4887	.8030	.6894
4AL	3AL:						
Mean <i>x</i>	.0997	.1013	.1076	.1252	.1339	.1643
 <i>y</i>	.0907	.0695	.0759	.0858	.0915	.1108
SD <i>x</i>	.0082	.0090	.0097	.0077	.0107	.0133
 <i>y</i>	.0070	.0072	.0076	.0050	.0064	.0080
<i>r</i>7930	.5200	.7153	.6464	.2722	.5312
6AL	5AL:						
Mean <i>x</i>	.0952	.0941	.1047	.1194	.1223	.1412
 <i>y</i>	.0842	.0889	.0951	.1095	.1089	.1249
SD <i>x</i>	.0064	.0083	.0069	.0067	.0070	.0107
 <i>y</i>	.0061	.0060	.0072	.0072	.0098	.0102

See footnotes at end of table.

Table A-7.—Means, standard deviations (SD), and coefficients of correlation (*r*) for the 11 pairs of characters measured in males of the 6 flea beetle species—Continued

[Millimeters]

Correlated characters ¹		<i>Disonycha argentinensis</i> (<i>n</i> =6)	<i>Agasicles hygrophila</i> (<i>n</i> =42)	<i>Agasicles connexa</i> (<i>n</i> =10)	<i>Agasicles interrogationis</i> (<i>n</i> =18)	<i>Agasicles vittata</i> (<i>n</i> =23)	<i>Agasicles opaca</i> (<i>n</i> =28)
<i>x</i>	<i>y</i>						
6AL	5AL—Continued:						
<i>r</i>8788	.7357	.5425	.5868	.5576	.5833
7AL	7AW:						
Mean	<i>x</i>	.0867	.0921	.1029	.1055	.1126	.1390
	<i>y</i>	.0548	.0514	.0572	.0504	.0537	.0857
SD	<i>x</i>	.0076	.0055	.0072	.0057	.0086	.0126
	<i>y</i>	.0024	.0037	.0028	.0029	.0031	.0072
<i>r</i>1936	.5436	.3984	.2907	−0.2230	.2968
PyW	PyL:						
Mean	<i>x</i>	.7056	.7354	.7441	.7982	.886	1.019
	<i>y</i>	.2886	.2525	.2387	.2470	.3412	.3649
SD	<i>x</i>	.0484	.0410	.0368	.0309	.0497	.0475
	<i>y</i>	.0237	.0471	.0541	.0398	.0543	.0788
<i>r</i>1149	.1375	.5286	−.0992	.2479	−.0398

¹Character abbreviations are identified in table 4. The measurements are illustrated in fig. 46.

Table A-8.—Means, standard deviations (SD), and coefficients of correlation (*r*) for the measurements of pronotal width (PrW) and length (PrL) of the combined vittate *Agasicles* species¹

[Millimeters]

Correlated characters PrW (<i>x</i>) and PrL (<i>y</i>)		Females (<i>n</i> =82)	Males (<i>n</i> =93)
Mean	<i>x</i>	1.2596	1.1601
	<i>y</i>	.9696	.9103
SD	<i>x</i>	.0796	.0753
	<i>y</i>	.0647	.0686
<i>r</i>8738	.8338

¹*Agasicles hygrophila*, *A. connexa*, *A. interrogationis*, and *A. vittata*.

Table A-9.—Composition of measured samples of *Agasicles opaca* supplemented in 1975 and divided into three geographic forms

Flea beetle	Number measured		Locality	<i>Alternanthera</i> host-plant species	Unused preserved specimens
	♀	♂			
Paraguay River form (<i>n</i> =37♀, 37♂). ¹	2	1	Shallow, pristine lagoons along Riachuelo Antiquera above Puerto Antiquera.	<i>A. hassleriana</i>	0
Do ¹	10	10	Shallow, clear lagoons below Puerto Antiquera do	0
Do ¹	10	11	Turbid lagoons, disturbed by cattle, near Barranqueras.	<i>A. hassleriana</i> and <i>A. philoxeroides</i> .	0
Do ²	6	2	Ditches with high biochemical oxygen demands, east side, Formosa, Formosa Province, Argentina (terra firma).	<i>A. philoxeroides</i> . . .	0
Do ²	1	1	Dry lagoons along Paraguay River opposite Asunción, Paraguay.	<i>A. hassleriana</i> and <i>A. philoxeroides</i> .	0
Do ²	0	0	Disturbed pond near Luque, Paraguay (terra firma)	<i>A. philoxeroides</i> . . .	3
Do ²	1	0	Shallow backwater of Lago Ypacaraí west of Luque, Paraguay (terra firma). do	0
Do ²	8	6	Shallow, turbid roadside ponds near Paraguay River and north of Asunción, Paraguay (terra firma).	<i>A. hassleriana</i>	0
Do ²	0	6	Backwaters along Paraguay River at Corumbá, Mato Grosso State, Brazil.	<i>A. hassleriana</i> and <i>A. philoxeroides</i> .	0
Plains of Mojós form (<i>n</i> = 15 ♀, 15 ♂).	15	15	Shallow ponds scattered over Plains of Mojós east of Trinidad, Beni Department, Bolivia.	<i>A. hassleriana</i>	11
Lower Amazon River form (<i>n</i> =18 ♀, 15 ♂).	12	12	Lago Careira, clear-water lagoon of the Amazon flood plain, below Manaus, Amazonas State, Brazil.	<i>A. hassleriana</i> , <i>A. philoxeroides</i> , and <i>A. sessilis</i> .	0
Do	6	3	Clear, pristine "varzea" lagoon of the Amazon flood plain near Monte Alegre, Pará State, Brazil.	<i>A. hassleriana</i>	0

¹Below confluence of Paraguay and Paraná Rivers, Chaco Province, Argentina.

²Above confluence of Paraguay and Paraná Rivers.

Table A-10.—Means, standard deviations (SD), and coefficients of correlation (r) for the 11 pairs of characters measured in females of 3 geographic forms of *Agasicles opaca*
[Millimeters]

Correlated characters ¹		Paraguay River form ($n=37$)	Plains of Mojos form ($n=15$)	Lower Amazon River form ($n=18$)	Correlated characters ¹		Paraguay River form ($n=37$)	Plains of Mojos form ($n=15$)	Lower Amazon River form ($n=18$)
x	y				x	y			
PrW PrL:									
Mean x	1.9446	1.9620	2.0124	AL MTL:		3.3102	3.3846	3.3939
	y	1.3925	1.4443	1.5079	Mean x	1.6671	1.6786	1.6726
SD x	.1287	.0966	.0811	SD x	.1799	.1480	.2357
	y	.0927	.0469	.0619		y	.1083	.1015	.1154
r8587	.4883	.6658	r7853	.3966	.6317
EL EW:									
Mean x	5.0480	4.9883	5.3944	4AL 3AL:		.4118	.4193	.4326
	y	3.2428	3.2431	3.4100	Mean x	.2817	.2679	.2994
SD x	.3052	.2403	.2817	SD x	.0307	.0317	.0422
	y	.2729	.1170	.1794		y	.0216	.0127	.0297
r7078	.4335	.9007	r5483	.4072	.5848
BL BTh:									
Mean x	7.0122	6.9475	7.7778	5AL 6AL:		.3537	.3807	.3825
	y	2.2601	2.3582	2.4472	Mean x	.3268	.2451	.3523
SD x	.4427	.2695	.4930	SD x	.0264	.0218	.0392
	y	.1604	.0701	.1064		y	.0211	.0174	.0234
r7929	.4378	.4026	r4992	.1525	.6214
HW HL:									
Mean x	1.2402	1.2410	1.3051	7AL 7AW:		.3560	.3680	.3929
	y	.6344	.6482	.6612	Mean x	.2261	.2145	.2360
SD x	.0489	.0445	.0600	SD x	.0241	.0234	.0343
	y	.0237	.0383	.0570		y	.0262	.0165	.0248
r4760	.3828	.1894	r6817	.4632	.8466
IOW IAW:									
Mean x	.7465	.7487	.7801	PyW PyL:		1.1431	1.1921	1.1830
	y	.2452	.2618	.2748	Mean x	.5704	.6243	.5342
SD x	.0410	.0386	.0336	SD x	.0734	.0508	.0440
	y	.0216	.0271	.0143		y	.0637	.0711	.0690
r4610	.3986	.2866	r2382	-.4854	.2597
U2W U1W:									
Mean x	1.1957	1.1484	1.1188					
	y	.2597	.2487	.4376					
SD x	.0865	.0582	.0815					
	y	.0606	.0780	.0751					
r0441	-.4639	.5795					

¹Character abbreviations are identified in table 4. The measurements are illustrated in fig. 46.

Table A-11.—Means, standard deviations (SD), and coefficients of correlation (r) for the 11 pairs of characters measured in males of 3 geographic forms of *Agasicles opaca*
[Millimeters]

Correlated characters ¹		Paraguay River form (n=37)	Plains of Mojos form (n=15)	Lower Amazon River form (n=15)
x	y			
PrW PrL:				
Mean x	1.8086	1.8088	1.9264
	y	1.3012	1.3912	1.4941
SD x	.0747	.0656	.0801
	y	.0686	.0570	.0532
r7366	.8105	.8233
EL EW:				
Mean x	4.6332	4.6740	5.1666
	y	2.8461	2.9185	3.1300
SD x	.3072	.1977	.3309
	y	.1574	.1155	.1533
r7285	.8159	.8506
BL BTh:				
Mean x	6.3504	6.4397	6.9467
	y	2.0315	2.0705	2.2667
SD x	.3763	.3504	.2615
	y	.1273	.0899	.0919
r6143	.6339	.7972
HW HL:				
Mean x	1.1906	1.1938	1.2590
	y	.5951	.6203	.6203
SD x	.0547	.0152	.0500
	y	.0469	.0205	.0538
r6537	.0257	.3990
UOW IAW:				
Mean x	.7107	.7122	.7639
	y	.2236	.2322	.2513
SD x	.0403	.0323	.0404
	y	.0367	.0248	.0179
r3246	.5978	.8354
U2W U1W:				
Mean x	1.0598	1.0897	1.0790
	y	.2605	.2485	.3807
SD x	.0772	.0615	.0583
	y	.0519	.0647	.0400
r	-.0682	.0705	-.0314

Correlated characters ¹		Paraguay River form (n=37)	Plains of Mojos form (n=15)	Lower Amazon River form (n=15)
x	y			
AL MTL:				
Mean x	3.3831	3.4221	3.3831
	y	1.6144	1.5735	1.6144
SD x	.2038	.1207	.2038
	y	.1077	.0726	.1077
r8707	.6701	.8707
4AL 3AL:				
Mean x	.4214	.4199	.4193
	y	.2939	.2699	.3700
SD x	.0417	.0205	.0219
	y	.0258	.0200	.0255
r5594	.4696	.3262
5AL 6AL:				
Mean x	.3670	.3825	.4193
	y	.3296	.3523	.3700
SD x	.0277	.0236	.0219
	y	.0213	.0151	.0255
r6741	.3992	.3262
7AL 7AW:				
Mean x	.3614	.3659	.4154
	y	.2264	.2137	.2437
SD x	.0271	.0204	.0259
	y	.0245	.0117	.0110
r5472	-.0031	.4413
PyW PyL:				
Mean x	1.0611	1.1151	1.1409
	y	.4044	.4049	.4094
SD x	.0488	.0627	.0502
	y	.0571	.0486	.1024
r2091	.2712	-.3903

¹Character abbreviations are identified in table 4. The measurements are illustrated in fig. 46.

Specific Names Referred to in Text, With Authors

Agasicles:

connexa (Boheman)
hygrophila Selman and Vogt
interrogationis (Clark)
opaca Bechyné
vittata Jacoby

Agromyza alternantherae Spencer

Alternanthera:

ficoidea (L.) R. Br.
halimifolia (Lam.) Standl.
 ex Pittier
hassleriana Chod.
kurzii Schinz ex Pedersen
maritima (Mart.) St. Hil.
obovata (M. and G.) Killip
paronychioides St. Hilaire
philoxeroides (Mart.) Griseb.
pungens H. B. K.
reineckii Briq.
repens (L.) Steud.
sessilis (L.) R. Br.
tetramera Fries

Altica:

foliacea LeConte
litigata Fall
marevagans Horn

Amynothrips andersoni O'Neill

Anolis chrysolepis Duméril and Bibron

Beta vulgaris L.

Chenopodium album L.

Coleomegilla quadrifasciata Schönh.

Disonycha:

argentinensis Jacoby
bicarinata Boheman
camposi Barber
collata (F.)
conjugata (F.)
conjuncta Germ.
eximia Harold
glabrata (F.)
limbicollis (Le Conte)
pennsylvanica (Illiger)
politula Horn
procera Casey
prolixa Harold
recticollis Jacoby
triangularis (Say)
uniguttata (Say)
xanthomelas (Dalman)

Drosophila melanogaster Meig.

Erynephala maritima (Le Conte)

Herpetogramma bipunctalis (F.)

Iresine diffusa H. and B.

Lebia:

analis Dejean
concinna Brullé

Lebia—

Continued:

securigera Chaudoir
viridipennis Dejean

Ludwigia peploides (H. B. K.) Raven

Lymantria dispar (L.)

Lysathia:

flavipes (Boheman)
ludoviciana (Fall)

Melanagromyza:

alternantherae Spencer
marellii (Brethes)

Musca domestica L.

Oenothera biennis L.

Ophiomyia sp. poss. *buscki* (Frost)

Phaedon (*Paraphaedon*)

tumidulus Germar

Philoxerus:

portulacoides St. Hil.
vermicularis (L.) R. Br.

Phoenicia sericata Meigen

Pyrrhalta (*Galerucella*)

nymphaeae (L.)

Sagra femorata (Drury)

Spinacia oleracea L.

Stellaria media (L.) Cyrillo

Trianthema portulacastrum L.

Vogtia malloi Pastrana

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